EXPERIMENTAL TAXONOMY

Thesis

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PREFACE

The accompanying series of papers embodies an endeavour to express in taxonomic terms the units established by experimental analyses of wild and cultivated populations. At the outset I should like to emphasise that the taxonomic treatment advocated in the following pages is not antagonistic to traditional methods of classification. Experimental Taxonomy, as its title implies, is based upon experimentally ascertainable facts, and when such evidence is lacking classificatory treatment must perforce follow another technique. Experimental Taxonomy, therefore, is actually complementary to Traditional Taxonomy and will ultimately, I hope, provide an additional focus for evolutionary discussion.

In arranging the papers I have given precedence to those bearing on the study of wild populations. This, I believe, is the most logical order since the more or less artificially controlled methods of raising and maintaining economically valuable populations are essentially repetitions of the processes operating naturally in the wild. Undoubtedly

such an arrangement somewhat interrupts the chronological sequence of ideas, but this defect is probably more than balanced by the considerations outlined above. Finally it will be noticed that one of the papers in the Plantago series has been written in collaboration with two of my colleagues. This paper has been included here because it forms an integral part of the series as it is the only one containing a detailed account of the technique employed throughout the investigations.

C O N T E N T S.

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EXPERIMENTAL DELIMITATION OF SPECIES

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(With 1 figure in the text)

CONTENTS

I. Introduction

The species of Linné have received much adverse criticism on the grounds that they are merely conventional units arbitrarily manufactured, for the sake of convenience, from morphological observations. There is no doubt that, even for the delimitation of the larger groups, the employment of the morphological criterion has been carried to extremes, but, since structural variation is the visible manifestation of genetic constitution, it is not surprising that the Linnean grouping may coincide with the grouping of the geneticist. [redacted]. The inadvisability of basing relationships on purely morphological data is clearly demonstrated by the work of Müntzing (1930) on the genus *Galeopsis*. "The representatives of sub-genus *Tetrahit*, occurring in Austria,

Ambiguity in the wording of the deleted sentence was only realised after publication. The following version conveys the meaning which was originally intended:-
With regard to the minor infra-specific units, however, a system of classification based entirely on morphological distinctions and resemblances may, from an evolutionary point of view, supply appellations which are of little or no significance

have been closely studied by Porsch (1903). The final results of this morphological investigation are conclusions concerning the relationship and descent of the four species in this sub-genus. *G. Tetrahit* and *bifida* are regarded as primitive and distinctly different types from which *pubescens* and *speciosa* respectively have gradually evolved. *G. bifida* and *speciosa* occupy the same branch in the genealogical tree, *Tetrahit* and *pubescens* another." Müntzing goes on to say "The present investigations have resulted in entirely different conclusions. *G. pubescens* and *speciosa* form one natural group, *Tetrahit* and *bifida* another. Most probably the latter group has originated from the first one by means of species hybridisation and chromosome summation" (p. 329).

The taxonomic position of "varieties" is even more vague than that of species. Since varietal differences are usually considered to be less distinct than those between species, the varietal diagnostic characteristics are masked to an even greater degree by environmental influences. It seems to be the case that varietal or even specific names are sometimes appended to single herbarium specimens because they are found to differ in some minor point from the general description of the group to which they belong. In such instances the application of names is of little taxonomic importance, for if such procedure were to be carried to its ultimate conclusion almost every genotype, and every clonal modification of an individual, would also deserve varietal or sometimes specific rank. The study of the individual organism is outside the realm of a descriptive systemisation based on the examination of dead specimens, since the naming of a few of the many possible combinations of characters as exhibited by individuals, without reference to the plasticity or inheritance of such characters, cannot be of value in taxonomy. Further the purely morphological differentiation of groups of individuals is not invariably effective, since morphologically similar forms may have different physiological reactions, e.g. the physiological strains of mistletoe, *Viscum album* (Tubeuf, 1923, pp. 100–101, 661–672). The morphological criterion alone, therefore, cannot be accepted as supplying a complete system of classification.

Du Rietz, in a recent paper, has re-defined the terms *species*, *sub-species* and *variety*, but, since his grouping depends mainly on morphological differences between geographically isolated populations, certain isolated populations of minor significance will assume an exaggerated value and attain the arbitrary status of separate species as is indicated by the following quotation (Du Rietz, 1930,

p. 364): "If all individuals of one population differ constantly, but very slightly, from those of the others, many taxonomists will treat the two populations as parts (sub-species or varieties) of one species, while others (and among them myself) will keep them apart as separate species." According to the literature, such a case "appears to be represented by the middle European *Pinus cembra* and the north-east European and west Siberian *Pinus sibirica*, by many authors (and also by myself in a previous paper, cf. Du Rietz, 1930, pp. 320–321), treated as mere sub-species or even as varieties of one species." Although Du Rietz recognises "the taxonomic importance of the lines or zones of discontinuity formed in a series of biotypes by geographical, ecological or physiological isolation" (p. 413), yet he apparently disregards (cf. pp. 352, 376, 399) the selective effect of environmental conditions on a genotype complex, as is evidenced by his statement "I have only talked of the process of differentiation by means of automatic reduction of polymorphy, *because no other process appears to be needed to explain what we see in nature*, and because this is the only process about which we know anything with full certainty." (For a further criticism of Du Rietz' paper see Müntzing, Tedin and Turesson, 1931.)

Valuable as the researches of the geneticist may be in exposing the artificial nature of the morphological system of classification, it must always be borne in mind that the ultimate genetical units are analytic rather than synthetic. If the systematist were to adopt the extreme view of Lotsy (1916, p. 23) that "a species consists of the total of individuals of identical constitution unable to form more than one kind of gametes," he would be put to much trouble to find even a single species in nature. It is extremely doubtful, as pointed out by Drummond (1927) in a review of the species problem, whether the ideal homozygous individual has ever been isolated even under controlled conditions. When the 1916 concept of Lotsy is applied to obligatory allogamous populations it obviously fails. The species of Lotsy, therefore, cannot be taken as a general basis of systematic classification, although such units are much to be desired for genetical and other experimental research.

The concept of Turesson, outlined in 1922 and amplified in 1929, appears to the present writer to be a constructive attempt to place the grouping of organisms on a more natural basis. Turesson's system is not dependent on one particular line of enquiry but embraces the results of morphological, genetical, ecological and cytological investigation. He points out (1929) that in nature units of different

degree occur which make it impossible to reach one standard definition of the "species."

The groups given by Turesson are as follows:

Coenospecies: "A population complex the constituents of which group themselves in nature in species units of lower magnitude on account of vitality and sterility limits having all, however, a common origin so far as morphological, cytological or experimental facts indicate such an origin." (Turesson, 1929, p. 333.)

Agamospecies: "An apomict population the constituents of which, for morphological, cytological or other reasons, are to be considered as having common origin." (Turesson, 1929, p. 333.)

Ecospecies: "An amphimict population the constituents of which in nature produce vital and fertile descendants with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population." (Turesson, 1929, p. 333.)

Ecotype: "The product arising as a result of the genotypical response of an ecospecies to a particular habitat." (Turesson, 1922, p. 345.)

In the present paper the Linnean species *Phleum alpinum* and *P. pratense* have been grouped according to the terminology of Turesson. The experimental results of the investigation have been published elsewhere (Gregor and Sansome, 1930), but it was thought advisable for purposes of clarity to give a brief summary in this paper. The classification outlined in the following pages has been proposed, not with the intention of advocating its general application, but as an example that indicates the possibilities of a natural system based on data of which morphological differentiation is not the only determining factor.

II. Examination of *Phleum* material

(*a*) *Groups within* Phleum pratense *L.* From a study of various populations growing in culture at the Scottish Plant Breeding Station it has become apparent that this Linnéan species contains two distinct groups. These have been distinguished by the terms Group I and Group II (Gregor and Sansome, 1930). All attempts to obtain inter-group hybrids have so far resulted in failure. Cytological evidence[1] has confirmed this grouping and demonstrated the fact

[1] The cytological examination of the *Phleum* material mentioned in this paper has been made by Dr F. W. Sansome, of the John Innes Horticultural Institution, London.

that Group I is hexaploid ($2n = 42$) and that Group II is diploid ($2n = 14$).

(*b*) *Groups within* Phleum alpinum *L.* Here also two groups have been distinguished. Material of Scottish origin has proved to be tetraploid ($2n = 28$), while plants of a population from Continental Europe have been shown to possess the diploid ($2n = 14$) number of chromosomes.

Group inter-relationship based on hybridisation results

Groups I and II of the species *P. pratense* L. are inter-sterile. It has, however, been found possible to cross both *pratense* groups with the tetraploid form of *P. alpinum* L., but the facility of hybridisation differs greatly for the two matings. From *P. pratense* $6n \times$ *P. alpinum* $4n$ only one sterile pentaploid plant has been obtained, while *P. pratense* $2n \times$ *P. alpinum* $4n$ has yielded almost sterile triploids in considerable numbers. These triploid plants yielded forty-six "seeds," only four of which germinated, giving rise to four hexaploid plants of varying fertility. One of these artificial hexaploid plants has been successfully crossed with the natural Group I hexaploid, giving 161 hybrid plants, many of which are both male- and female-fertile.

It has been tentatively suggested (Gregor and Sansome, 1930) that *P. pratense* Group I ($6n$) may be the result of natural hybridisation of *P. pratense* Group II ($2n$) with some other plant, in a manner analogous to that described for the artificially produced hexaploid, i.e. by the doubling of the chromosomes in gametes of the hybrid *P. pratense* Group II ($2n$) $\times$ *P. alpinum* $4n$. Whether or not this surmise is correct may be disclosed by future research, but it can be stated definitely that the sterility gap between *P. pratense* Group I ($6n$) and Group II ($2n$) has been successfully bridged by the employment of the tetraploid form of *P. alpinum* L.

The cross *P. pratense* Group II ($2n$) $\times$ *P. alpinum* $2n$ has yielded two sterile hybrids, the female parent being one of those employed in some of the previously described matings.

Fig. 1 gives a diagrammatic representation of the various crosses.

Ecological significance of groups

The two Linnean species *P. alpinum* and *P. pratense* are apparently ecological units of considerable importance; although in Scotland *P. alpinum* L. only occupies habitats at relatively high altitudes, yet in more northerly latitudes the species descends almost to sea level.

(*a*) *P. alpinum* L. *P. alpinum 4n* has never been found in Britain by the present writer under 2000 feet, yet the species can be cultured at low elevations with some degree of success provided that conditions

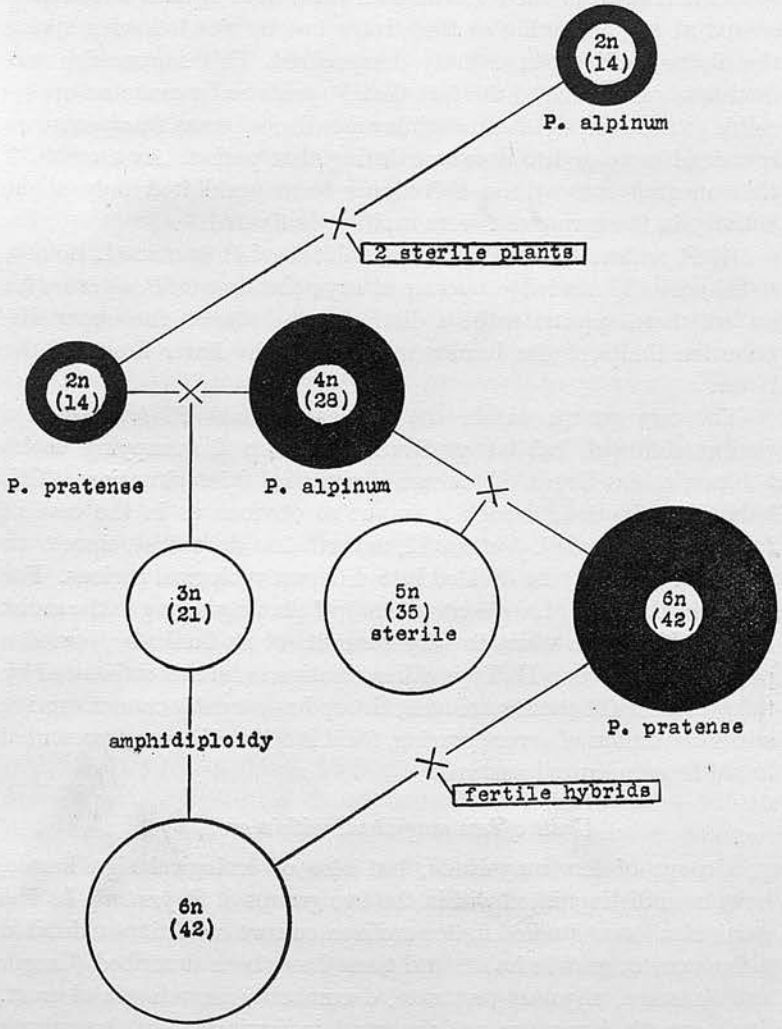

Fig. 1. Diagrammatic representation of the *Phleum* crosses. The blackened circles indicate forms which occur in nature.

are not too dry and that competition with lowland plants is prevented. It has more than once been observed in the field that the species did not descend below a certain limit even where facilities were

available for transport of the seeds, e.g. by water-courses, from upland situations to localities of less altitude. In culture when equal numbers of seeds of *P. pratense* 6*n* and *P. alpinum* 4*n* were mixed and sown in the experimental field, both species were represented at the beginning of the winter but by the following spring the alpine species had entirely disappeared. This suppression was doubtless partly due to the fact that *P. pratense* 6*n* made an appreciable growth throughout the winter months, whereas *P. alpinum* 4*n* remained more or less dormant during that period. As a result of this unequal competition the alpine forms exhibited only slight activity in the spring and were rapidly eliminated.

(*b*) *P. pratense* L. In Britain the habitats of *P. pratense* L. do not, to the writer's knowledge, overlap at any point those of *P. alpinum* L., in fact there appears to be a distinct gap between the upper distribution limits of the former species and the lower limits of the latter.

The two groups within the Linnean species *P. pratense* also exhibit different habitat preferences, Group I occupying moist habitats while Group II occurs mainly in drier situations. This habitat distinction, though it is not so obvious as in the case of *P. alpinum* L. and *P. pratense* L., nevertheless does exist, since even a limited area may be divided into different ecological regions. For example, the writer has observed Group I plants growing in the moist bottom of a ditch while the dry summits of its banks supported a population of Group II. Type differentiation is further influenced by the prevalence of grazing animals; Group I apparently cannot survive under conditions of severe grazing, for it is seldom if ever represented in old heavily grazed pastures.

Units of less magnitude within groups

Groups of less magnitude, but also of ecological significance, have been distinguished within the two groups of *P. pratense* L. The particular forms studied under uniform culture conditions exhibited differences in growth habit, and these have been described (Gregor and Sansome, 1930) as prostrate, decumbent, ascending and erect. Such growth forms are not dispersed indiscriminately throughout their distribution area but are represented in various proportions in different habitat populations, the general growth habit of each population bearing a relationship to the prevailing conditions of grazing.

III. CLASSIFICATION OF THE *PHLEUM PRATENSE-ALPINUM* GROUP.

Ascherson and Graebner (1899) treat the two Linnean species *P. pratense* and *P. alpinum* as two sub-species, which they name *P. vulgare* and *P. alpinum*; Hegi (1906), however, prefers to consider *P. pratense* L. and *P. alpinum* L. as two distinct species. These authors in common appreciate the necessity for differentiation between the *pratense* and *alpinum* groups, and this division is understandable on morphological grounds. It is equally true, however, that the *2n* and *6n* forms of *P. pratense* L. can be distinguished by an important difference in their chromosome complexes involving incompatibility, and that these groups are consequently worthy of specific or sub-specific designation. Under a system of classification based solely on morphological differences the advisability of separating these groups, now included in the Linnean species *P. pratense*, is not obvious. Further, such a separation would be extremely difficult, since even under uniform culture conditions the morphological differences of possible taxonomic value are more quantitative than qualitative. If, however, the division is based on the results of cytological, ecological, genetical, and morphological investigations the groups become sharply defined and form units of considerable evolutionary significance.

It appears possible that variety *typicum* A. and G. (Ascherson and Graebner, 1899) and variety *typicum* Beck (Hegi, 1906) have been described from specimens of the hexaploid form, but both descriptions are sufficiently vague to preclude an exact determination. There is also an indication that var. *nodosum* A. and G. and var. *nodosum* (L.) Richt. (Hegi, 1906) correspond to the diploid form, but again the morphological descriptions do not permit of a definite diagnosis. Several sub-varieties of var. *typicum* and var. *nodosum* are enumerated by Ascherson and Graebner (1899) and by Hegi (1906); these, like the varieties, are differentiated on small morphological characters many of which are very liable to modification by the prevailing environmental conditions. It is obviously of little value to give the sub-varietal name *serotinum* St Lager (Hegi, 1906) to a form with the following description: "Stem upright, often not distinctly thickened, 2–3 dm. high. Panicle long up to 8 cm., cylindrical, not more than 5 mm. thick. The spikelets firmly adpressed. Barren-glume point fairly short." Such a name is of slight taxonomic importance in a group of plants in which cross-fertilisation is to a great extent obligatory. It would seem, therefore, that these sub-

varieties represent only a few of the many possible genetic combinations within their respective groups.

As previously mentioned the present writer has recognised four growth forms within the species *P. pratense* L. (Gregor and Sansome, 1930, Plates XV and XVI), and these group themselves into populations bearing a definite relationship to the prevailing environmental conditions (in this case the biotic factors) of their respective habitats. It must be remembered, however, that such habitat populations form intra-crossing groups, the components of which need not necessarily be homozygous for their distinguishing character or characters, since phenotypic characters may determine their survival in a particular situation. It has been found that when plants of a population of *Lolium perenne* L., which had been subjected to severe grazing in the wild, were examined in culture they exhibited a phenotypic similarity, but that when they were self-fertilised under controlled conditions certain of them proved to be heterozygous for their particular growth-habit characters (Gregor and Sansome, 1927). Habitat types, therefore, may be regarded as the genotypical response of a group of greater magnitude to particular environmental conditions—ecotypes (Turesson, 1922).

Thus the position at present is as follows:

COENOSPECIES

PHLEUM PRATENSE—ALPINUM

ECOSPECIES

P. pratense diploidium	*P. alpinum diploidium*
P. pratense hexaploidium	*P. alpinum tetraploidium*

ECOTYPES[1]

P. pratense 2*n prostratum*
" *decumbens*
" *ascendens*
" *erectum* (Ecotypes of *P. alpinum* also exist)
" 6*n decumbens*
" *ascendens*
" *erectum.*

NOTE: Although the polyploid *P. alpinum tetraploidium* may only represent the duplication of chromosome sets within the diploid form, it, nevertheless, constitutes an important ecological and evolutionary unit.

[1] For descriptions and figures, see Gregor and Sansome 1930, pp. 375, 377, 378, Text-fig. 1 and Pls. XV, XVI.

If subsequent research should prove that the existence of habitat populations is a phenomenon of general occurrence, the ecotype, and not the homozygous individual, would constitute the smallest unit of taxonomic value in cross-fertilising groups.

As previously mentioned it has been possible to connect *Phleum alpinum* 4*n* with both forms (2*n* and 6*n*) of *P. pratense* L., and to bridge the sterility gap between these forms by employing hexaploid individuals (Fig. 1). It may therefore be concluded that the Linnean species *P. pratense* and *P. alpinum* constitute a single natural group: to employ Turesson's terminology—a coenospecies, comprising several groups of lesser magnitude—ecospecies, and that these latter contain still smaller units of ecological significance—ecotypes.

Although cytological data have a direct bearing on the separation of groups, chromosome number alone cannot be regarded as the infallible criterion of taxonomical position, e.g. *Viola canina* (Clausen, 1931).

IV. Discussion and conclusions

The fact that closely "allied" species of the same genus frequently occupy the same distributional area cannot be assumed to imply that such "species" have similar environmental preferences, since each may populate different ecological positions within the same geographical area. The occupation of different habitats within Britain is clearly illustrated by the ecospecies *P. pratense diploidium*, *P. pratense hexaploidium* and *P. alpinum tetraploidium*. In this area *P. alpinum tetraploidium* is separated from both *P. pratense diploidium* and *P. pratense hexaploidium* by an altitude barrier. In the case of the two latter ecospecies the habitat distinction is not so pronounced, nevertheless these two ecospecies populate different, though sometimes adjacent, lowland habitats.

The smaller units of ecological significance (ecotypes) which have so far been studied within the ecospecies *P. pratense diploidium* and *P. pratense hexaploidium* have reference only to grazed and ungrazed habitats; the decumbent form predominates in the former and the erect in the latter, such differentiation being more complete under extreme environmental conditions. It is evident, therefore, that within the ecological distributional area of both ecospecies, habitat populations, bearing a relationship to the prevailing conditions of their respective habitats, have been separated from the ecospecies complexes.

Provided that local environmental differences are sufficiently dis

tinct, the establishment of different habitat populations may result even in the absence of spatial isolation between interfertile populations (Gregor, 1930). Observations on *Phleum* and other plants indicate that the more extreme the environmental conditions of a habitat the more highly specialised are the inhabiting populations. It is to be expected, therefore, that the populations represented at the limits of environmental distribution will be more specialised, but not necessarily more "advanced," than those occupying the area of optimum conditions. This, combined with the probability that the genotype complex is not the same at all points on the periphery of the distribution area, must account for a considerable number of the "forms," "varieties," "sub-species" and "species" of doubtful significance which are reported in the botanical literature.

Although it has been demonstrated that population differentiation is influenced by the edaphic (Turesson, 1922 and 1927), the biotic (Gregor and Sansome, 1927 and 1930; Stapledon, 1928), and, when large areas are concerned, by the climatic factors of the environment (Turesson, 1930), yet there are instances of the occurrence of type differentiation in the absence of any such ecological selection. The chance introduction of different parts of a larger population into similar but isolated ecological regions may result in the establishment of distinct local populations, possessing peculiar characteristics which bear no apparent relationship to the prevailing conditions of their habitats. In such cases it is evident that the initial cause of the differentiation is not the same as that responsible for the establishment of ecotypes, inasmuch as the distinctions are maintained by mechanical barriers, instead of by selection due to environmental processes.

It is reasonable to suppose that on a continent, and on islands lately separated therefrom, where the distribution of an ecospecies is continuous, or where spatially separated populations of an ecospecies can be shown to be relics of a once continuous distribution, habitat types will be mainly differentiated as a result of the selective action of the environment. On the other hand, in areas isolated by effective natural barriers, for example oceanic islands and islands which have undergone depopulation within comparatively recent times (e.g. during a glacial period), chance introductions of unrepresentative parts of an ecospecies may result in the formation of distinctive habitat types, which are mainly due to mechanical isolation and not to subsequent environmental action. The occurrence of local races of mice in some adjacent islands of Scotland at least suggest such a contingency, although the possible local origin of these forms must not be altogether disregarded.

The following examples are taken from Robson's (1928) excellent review of the species problem: "*Microtus agrestis exsul* occurs on Arran, Jura, Mull, North and South Uist and on other islands, while on Muck a special variety *M. agrestis luchii* is found, and another variety *mial*, occurs on Eigg. Great Cumbrae has its own form of *Apodemus hebridensis*, but its shrew (*Sorex araneus*) is the mainland form. Shetland and Fair Isle have the same variety of *Apodemus fridariensis*, while the neighbouring island of Foula has its own variety (*thuleo*)" (p. 141).

"In the first place it seems very unlikely that, e.g. the divergence of *Microtus agrestis luchii* on Muck, is due to 'special conditions' realised on that island and nowhere else. Nothing short of an intensive ecological survey can of course provide a final answer to this suggestion. But it seems very improbable that Arran, Jura, Mull and North and South Uist are so identical ecologically and Muck so unique, that only on the latter was *M. agrestis exsul* subjected to adaptive modification or direct transformation by the environment" (p. 142). "My colleague, Mr Hinton, tells me that *Microtus* is not likely to be carried from island to island by man" (p. 143).

There is also a considerable amount of evidence which indicates that even within a limited area the flora may be greatly influenced by the presence of natural barriers which restrict free sexual reproduction. In the comparatively limited area of North-west Yunnan and Upper Burma (a district which is divided by several great parallel gorges) the species within certain genera exhibit geographical differentiation to a very marked extent, e.g. *Primula* and *Rhododendron*.

The geographical isolation of portions of species populations within the Yunnan-Burma region is a factor which is doubtless partly responsible for the very large number of *Primula* spp., approximately 300 species and sub-species, and *Rhododendron* spp., upwards of 500, described from the district. For these figures the writer is indebted to Professor Wright Smith and Mr Edgar Evans of Edinburgh.

There may, therefore, be at least two processes influencing the formation of local populations: (1) ecological selection causing the partial or complete separation of different habitat populations, (2) chance introduction into mechanically isolated areas where conditions do not prohibit the multiplication of the introduced organisms. These processes may either act separately or together, as would be the case if certain genotypic combinations were eliminated by the environmental factors at the time of arrival in the new areas.

The habitat types differentiated from their population mass as a result of mechanical isolation cannot be regarded as the ecotypes

defined by Turesson (1922). He, however, has employed the term *seclusion type* (Turesson, 1927) to indicate "units resulting from geographical chance isolation," and has demonstrated their apparent existence within a lowland ecotype of *Poa alpina*. It would, nevertheless, be difficult to regard seclusion types as independent taxonomic units divorced from ecotypes, since, in order to become established, they must of necessity be tolerant of the existing environmental conditions of their new habitat. Further, although the distinguishing characters may be the result of mechanical isolation, there may have been others which were eliminated subsequent to the initial introduction. Doubtless this statement applies not only to mechanically isolated populations, but to any fractional population where the fraction does not represent the whole genotype complex of the group of which it is a part.

Although it is impossible in the present state of knowledge to determine whether certain characters exhibited by habitat-populations have, or have not, some ecological value, yet it seems advisable to make a distinction, whenever possible, between characters which apparently have only a geographical significance, and those which are the result of the interactions of the plants and their habitat factors. In this connection the term *geo-ecotype* might be usefully employed to denote a unit, of ecotype status, the distinguishing features of which are suspected of possessing only a geographical significance.

V. SUMMARY

1. A system of classification based entirely on morphological distinctions and resemblances cannot do much more than supply to its smaller units an appellation of little or no evolutionary significance.

2. When the Lotsian (1916) conception of species is applied to wild material it obviously fails, in as much as it disregards the occurrence of cross-fertilisation which in many cases is obligatory. The species of Lotsy, therefore, cannot be taken as the bases of taxonomy although such units are much to be desired for genetical and other experimental research.

3. The concept of Turesson appears to the present writer to be a constructive attempt to place the grouping of organisms on a more natural basis. His system is not dependent on one particular line of enquiry, but embraces the results of morphological, cytological and experimental investigation.

4. Within the Linnean species *Phleum pratense* two intersterile groups (Group I and Group II) have been demonstrated. It has been possible to connect both these groups with *P. alpinum* L., and to

bridge the sterility gap between Group I and Group II. It may be concluded, therefore, that the Linnean species *P. pratense* and *P. alpinum* constitute a single natural group: to employ Turesson's terminology—a *coenospecies*, comprising several groups of less magnitude—*ecospecies*, and that these latter contain still smaller units of ecological significance—*ecotypes*.

5. If subsequent research proves that the existence of habitat populations is a phenomenon of general occurrence, then the ecotype and not the homozygous individual should constitute the smallest unit of taxonomic value in cross-fertilising groups.

6. It seems advisable to make a distinction, whenever possible, between populations possessing characters which apparently have only a geographic significance, and those in which the distinguishing features are the result of the selective influence of the habitat factors. In this connection the term *geo-ecotype* might be usefully employed to denote a unit of ecotype status, the distinctive characters of which are suspected of possessing only a geographical significance.

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EXPERIMENTS ON THE GENETICS OF WILD POPULATIONS.

I. *PLANTAGO MARITIMA.*

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(With Two Plates and One Text-figure.)

CONTENTS.

Introduction.

The present paper may be regarded as introductory to a study of the effects of environmental conditions on isolated populations of *Plantago maritima* L. in the British Isles. The particular aspects of the problem to be considered here are the general distribution of the species in Britain and the growth-forms which inhabit that area.

Any form of isolation which separates parts of a species-population from the mass undoubtedly aids in the formation of habitat types; further, the effect of environmental factors in bringing about local differentiation must also play an important part. It seems reasonable to assume that if a cross-fertilised species possessed a continuous distribution extending through a uniform environment, undivided by mechanical or other barriers to free sexual reproduction, the chances are small that such a population would be split into genotypically distinct groups because of the tendency to a general diffusion of the existing characters throughout the entire population. In nature, however, such a combination of conditions is rarely encountered, and local differentiation is usually attributed to some form of isolation or to the influence of the environment. Nevertheless, direct experimental evidence concerning the inherited differences between portions of a natural species-population is extremely limited.

Conclusions which have been based on experimentation conducted for a very limited period (a few generations) are sometimes utilised to elucidate problems connected with the inter-relationship of the plant and its environment. The experimental conditions, however, do not truly represent the natural conditions, for, in the wild, the interactions of plant and environment operate over a long period of time.

The research to which this paper forms an introduction represents an attempt to overcome the time-factor difficulty by means of a study, in culture, of parts of a species-population from different wild habitats. Each part will presumably have been subjected to the influence of a particular environment for many generations, and, by the examination of collections from isolated but apparently similar habitats, it should be possible to estimate the importance of isolation as a factor in the differentiation of local types.

Material.

For the purposes of the present investigation the species *P. maritima* has been utilised, since it possesses certain qualities necessary for a research of this nature:

(1) A continuous coastal and localised inland distribution in the British Isles.

(2) Cross-fertilisation as the normal means of sexual reproduction; in many cases obligatory, owing to a low degree of self-fertility.

(3) Characters which can be measured with some degree of accuracy.

Distribution of *P. maritima*.

The species occurs in Europe, Central Asia, America and in South Africa. The British population of *P. maritima* has been separated from the main mass of the species on the Continent for a very considerable time, and has, since its isolation, undergone further division into localised populations. Its distribution is continuous throughout the maritime regions, but inland it is decidedly scattered, being chiefly confined to high altitudes. Nevertheless it is incorrect to conclude that inland the species is restricted to the higher mountains, since the present writer has collected it from central Scotland at elevations of over 2500 feet and also as low as 400 feet.

If reference is made to the floral history of Britain, the discontinuous inland distribution of *P. maritima* can, at least partly, be explained. It is still a matter of considerable doubt whether, during the Pleistocene period, the flora of the British Isles was exterminated, or whether some

portion survived in the south of England during the period of maximum glaciation. It is, however, certain that the greater part of Scotland was denuded at that time of its previous flora, and the development of its present vegetation commenced only when the Ice Age was succeeded by more congenial climatic conditions. Matthews (1923, 1924) has demonstrated the lines of plant invasion into Britain from the European Continent, and he concludes that overland migration is mainly responsible for our present flora, although he believes that part of the flora survived the period of maximum glaciation, at least in the South of England. Chevalier (1923) suggests that the northward movement of species after the retreat of the ice had not been completed when the Channel was formed. Thus the further spread of Continental plants into England, except for occasional subsequent introductions, would be prevented by this natural barrier. Turrill (1927) holds that the flora of the islands of St. Kilda "as represented by the dominant heath moor types, survived the Ice Age in the islands, either these escaping glaciation owing to their oceanic position or plants continuing to exist on local nunataks." Turrill (1928): "That the same is true for the heath-moor flora, and one might add the aquatic and marsh flora, of Foula seems even more likely." Woodhead (1929) points out that, even at the glacial climax, there were parts of the Pennines free from ice. In his paper on the Pennine peats (1924) he suggests that "as the Southern Pennines was an unglaciated area during the Ice Age these moorland species would for the most part persist through that period," but, as he writes (1929), "we have no records preserved to us of the vegetation of the area at this early period." On the other hand Reid (1899) infers that, during the glacial climax, the flora of Britain was exterminated except in the south. He writes: "The result seems to have been the total blotting out of the flora over the area north of the Thames and Severn, with the possible exception of certain high hills which rose above the ice. Even these were probably so smothered with snow that only the steeper crags were bare in summer."

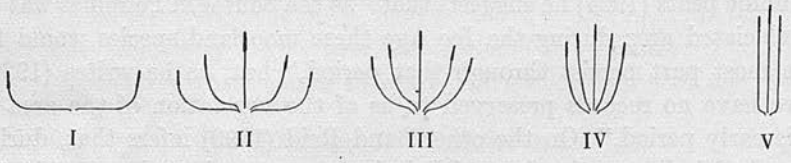
The difficulty of estimating the age of the flora of Britain is obvious. It is, however, the conditions prevailing during the period of maximum glaciation which are of importance in this connection, and whether the species *P. maritima* survived the extreme conditions of that period, as a nunatak species, is very doubtful.

The present inland distribution of *P. maritima* is, therefore, apparently a remnant of a former more general distribution. It is probable that this species followed the retreating ice at the close of the glacial

period, and, owing to its xerophytic nature, it would be well qualified to withstand the prevailing conditions of physiological drought; this supposition is borne out by the fact that the species is frequently associated inland, at high altitudes, with other plants of the sea shore. Presumably the British *P. maritima* originated from a continental stock which spread, by overland migration, over the greater part of the country in early post-Pleistocene times, subsequent environmental changes having been responsible for the present restricted inland distribution. There appears to be little doubt that competition with other species has exterminated *P. maritima* from the intermediate stations, since it can grow vigorously at low elevations under mesophytic conditions both in culture and in the wild, provided that competition is not excessive; this illustrates, as Salisbury (1929) remarks, the fact that plants grow not where they would but rather where they must.

Growth-forms.

The species *P. maritima* comprises many growth-forms which range from the decumbent to the erect. For purposes of identification they have been classified into five groups (Text-fig. 1), although actually there is no sharp line of demarcation between one form and the next in the series.



Text-fig. 1. Five types of habit of growth represented diagrammatically.

Form I (Plate I, No. 1). *Spikes*: restricted to periphery. *Scapes*: all markedly decumbent.

Form II (Plate I, No. 2). *Spikes*: general. *Scapes*: peripheral markedly decumbent, becoming erect towards centre of plant.

Form III (Plate I, No. 3). Similar to Form II but peripheral scapes less decumbent.

Form IV (Plate I, No. 4). *Spikes*: general. *Scapes*: peripheral sharply ascending.

Form V (Plate II, No. 5). *Spikes*: general. *Scapes*: erect.

The different combinations of characters, *e.g.* leaf length, leaf breadth, etc., exhibited by plants of the same growth-habit make the total number of forms in the species very extensive. Under natural conditions the

plants forming a habitat population may sometimes be so modified by extreme environmental conditions as to assume a phenotypic similarity which masks the presence of the various forms, and it is only by bringing such plants into the more congenial environment of the experimental garden that the differences in type between the members of the population become evident.

COLLECTION AND EXAMINATION OF MATERIAL.

Observations made on populations grown under controlled conditions have indicated that a culture of a population raised from seed collected in the wild, probably gives a better conception of the genotypical composition of that population than does a culture of plants collected in the mature state. In the latter case the phenotypical uniformity of the plants forming a population is sometimes exaggerated, owing to the suppression of certain phenotypes by the environmental conditions of the wild habitat. Moreover, for the comparison under a uniform environment of populations from distinct habitats, the cultures raised from seed have the advantage of developing under the experimental conditions from the time of sowing. In the case of collected plants, on the other hand, the uniform environment acts only from the time of transplantation and, as a result, the time required to nullify the modificatory influence of the previous environment is indefinite.

Under cultivation all the populations received similar treatment. The samples were sown in a greenhouse, and the seedlings were transplanted at an early stage of growth into boxes, whence they were transferred to the experimental garden; they were spaced 1·5 feet (46 cm.) apart in rows at 2 feet (61 cm.) intervals. As a result of this method the seedling death-rate was practically negligible. The populations were examined during both the first and second year of their growth.

When comparing the measurable characters of the populations the mean was taken as the average value for the character in question, since it gives weight to the extreme variations, and for this reason a greater significance was attached to this figure than to the mode. In comparing the means the differences were taken to be significant only when they exceeded five times the Standard Error of the difference. It may be concluded, therefore, that populations with means which differ by this amount do not form a homogeneous group, the variability being too high to result from the operation of chance alone.

Material in nature.

The present paper deals only with plants derived from a single locality on the east coast of Scotland. This area, though very limited in extent, was ecologically divided into two regions:

(1) Exposed rock immediately above the normal high-tide mark. The plants of *P. maritima* were sparsely distributed, and only occurred where small quantities of organic matter had accumulated. They resembled each other closely and were characterised by a dwarf, more or less decumbent, habit of growth.

(2) An adjoining grassy slope. *P. maritima* was here growing in a dense association, mainly composed of varieties of *Festuca ovina* L., which attained an average height of 9 inches. The majority of the plants of *P. maritima* exhibited the upright growth habit, but some type differentiation was in evidence.

Material in culture.

As previously mentioned the plants growing on the exposed rock were somewhat scattered, and this fact, in conjunction with the extreme environmental conditions, reflected adversely on seed production, with the result that the number of plants available for the culture experiments was limited to 50 from each habitat. Notwithstanding this scarcity of material in culture, sufficient evidence has been forthcoming to indicate that the plant populations from the two areas neither formed a homogeneous mass, nor differed so greatly as their parent populations. The plants were examined and measurements of certain characters made at intervals during a period of two years. The plants of each population were classified at the end of their second year's growth into the types previously described in this paper. The results expressed as percentages are given in Table I.

TABLE I.

Types within the populations.

	% of types in population	
Type	*P* 11 (grass)	*P* 12 (rock)
1	15	61
2	40	18
3	30	19
4	15	2
5	0	0

Table I shows the difference as regards habit of growth between the two populations. Although the typical Class 5 habit of growth was not

represented in either population, one plant of *P* 11 closely approached the required standard.

In Table II the measurements of the various characters are given; the leaf data are confined to the first part of this table and are followed by the scape and spike measurements. The headings leaf breadth and leaf length are self explanatory, but leaf height and leaf spread require some further qualification. The leaf height of a plant was taken to be the vertical distance from the ground level to the upper leaf limit, and the

TABLE II.

Leaf and scape measurements for populations P 11 *and* P 12.

Character	Population no.	Date of measurement	Range Min.	Range Max.	Mean	Difference between means	Coefficient of variability
Leaf measurements							
Breadth in mm.*	*P* 11	31. v. 28	7	17	10·3 ±0·40	2·4 ±0·53	25·4 ±2·94
	P 12	,,	4	14	7·9 ±0·35		32·8 ±3·41
	P 11	21. vi. 28	6	16	10·4 ±0·36	2·3 ±0·48	21·2 ±2·37
	P 12	,,	4	15	8·1 ±0·34		30·9 ±3·20
Length in cm.†	*P* 11	31. v. 28	15	36	23·6 ±0·70	1·8 ±0·90	19·2 ±2·15
	P 12	,,	12	37	21·8 ±0·59		19·6 ±1·90
	P 11	21. vi. 28	20	37	26·3 ±0·68	0·6 ±1·01	16·3 ±1·86
	P 12	,,	16	40	25·7 ±0·75		21·4 ±2·14
Height in inches	*P* 11	1. ix. 27	3	10	6·4 ±0·34	2·0 ±0·47	34·6 ±4·13
	P 12	,,	2	7	4·4 ±0·34		51·8 ±6·70
	P 11	15. v. 28	2	8	4·2 ±0·23	1·6‡ ±0·28	35·2 ±4·14
	P 12	,,	1	8	2·6 ±0·18		50·8 ±5·90
Spread in inches	*P* 11	1. ix. 27	10	28	18·1 ±0·62	0·5 ±0·79	22·1 ±2·46
	P 12	,,	10	23	17·6 ±0·50		19·4 ±2·06
	P 11	15. v. 28	9	21	15·9 ±0·43	1·4 ±0·60	17·7 ±1·99
	P 12	,,	9	22	14·5 ±0·42		21·9 ±2·15
Ratio spread/height	*P* 11	1. ix. 27	1·7	4·3	3·2 ±0·13	1·4‡ ±0·27	26·6 ±3·03
	P 12	,,	1·7	8·0	4·6 ±0·23		35·0 ±3·99
	P 11	15. v. 28	2·3	9·0	4·2 ±0·18	2·6‡ ±0·38	28·3 ±3·30
	P 12	,,	3·0	14·0	6·8 ±0·34		37·1 ±4·03
Scape measurements							
Length in inches	*P* 11	5. vii. 28	12	17	14·4 ±0·22	1·8 ±0·37	9·4 ±1·06
	P 12	,,	8	19	12·6 ±0·31		17·9 ±1·77
	P 11	1. viii. 28	13	19	15·2 ±0·23	1·8 ±0·42	9·6 ±1·08
	P 12	,,	8	19	13·4 ±0·36		19·7 ±1·94
Height in inches	*P* 11	1. ix. 27	7	18	11·5 ±0·50	2·6 ±0·73	28·8 ±3·30
	P 12	,,	4	18	8·9 ±0·54		39·4 ±4·83
	P 11	5. vii. 28	8	21	13·7 ±0·44	3·6‡ ±0·64	20·2 ±2·36
	P 12	,,	5	19	10·1 ±0·47		34·2 ±3·65
	P 11	1. viii. 28	8	21	15·9 ±0·44	4·4‡ ±0·72	17·7 ±2·04
	P 12	,,	5	22	11·5 ±0·57		36·6 ±3·94
Spread in inches	*P* 11	1. ix. 27	8	23	14·8 ±0·50	1·4 ±0·73	21·6 ±2·47
	P 12	,,	6	25	16·2 ±0·52		21·6 ±2·40
Ratio length/height	*P* 11	5. vii. 28	0·8	1·9	1·1 ±0·04	0·3‡ ±0·06	21·8 ±2·54
	P 12	,,	0·8	2·2	1·4 ±0·05		24·1 ±2·42
	P 11	1. viii. 28	0·8	1·7	1·0 ±0·03	0·3‡ ±0·05	18·0 ±2·08
	P 12	,,	0·8	2·2	1·3 ±0·05		26·2 ±2·67
Ratio spread/height	*P* 11	1. ix. 27	0·8	3·5	1·1 ±0·09	1·0‡ ±0·15	48·3 ±6·44
	P 12	,,	0·7	5·1	2·1 ±0·13		41·4 ±5·10

* The broadest leaf on each plant. † The longest leaf on each plant. ‡ Difference significant.

leaf spread was the greatest distance, across the plant, between the apices of opposite leaves. The scape measurements are those of the combined peduncle and rachis. The scape height is the vertical distance from the ground surface to the apex of the tallest spike, and the scape spread is the maximum distance through the centre of the plant between the apices of opposite marginal spikes.

From a comparison of the means of leaf height and scape height of the two populations, it is evident that there is a decided tendency towards a lower growth habit in the case of the rock population.

Although most importance is attached to the mean values, it would be inadvisable to disregard the figures given under the "range" column since it is these figures which indicate the types possessed by the populations. We see from the "difference between means" column that there is a significant difference between the leaf heights and the scape heights respectively for the two populations in their second year of growth. Nevertheless, from the "range" column of the same dates it is evident that the differences are not due to the absence of tall plants in the rock population, but to the preponderance of the tall type and the lack of low growth forms in the grass population. The difference in growth habit is perhaps more pronounced when the ratios leaf spread/leaf height, scape length/scape height, and scape spread/scape height respectively, are compared for the two populations; these ratio differences are significant according to the chosen standard. In culture, the mean leaf breadth for *P* 11 was greater than that for *P* 12, but the difference is not significant; the difference in leaf length is obviously not significant. Under the wild conditions, however, one of the most marked distinctions between the two populations was the leaf form. The leaves of the rock population were short and almost cylindrical (Plate II, fig. 6 *a*), while those of the grass population were long and dorsiventral, and exhibited obvious signs of etiolation. In transverse section the two leaf types were distinct. Plants which had been taken from the rock habitat and cultivated for a year lost their characteristic cylindrical leaves and became indistinguishable from plants collected from the grass habitat (Plate II, fig. 6 *b*). All the plants of populations *P* 11 and *P* 12, raised at Corstorphine, exhibited the dorsiventral leaf type, but variation in leaf succulence was observed. It was demonstrated that the fleshy habit of the leaves could be induced experimentally by watering the plants with a 3·5 per cent. solution of sodium chloride.

In addition to the examination of measurable characters, observations were made on the floral characters, the time of flowering, the leaf shape,

and the presence or absence of hairs on both the leaves and scapes, but, although considerable variation existed, no definite distinction between the two populations was found.

DISCUSSION AND CONCLUSIONS.

It is unlikely that a part of a species-population will represent the genotypic composition of the whole, and, therefore, when a part is prevented from crossing with the bulk of the species it may be expected that the separated portion will differ in some way from the species as a whole. The number of agencies, however, involved in the differentiation of species and populations within species must be large, and the assumption is unwarranted that any one of these can be, to the exclusion of all others, the sole controlling factor. The influence of environment is doubtless of considerable importance, but the interactions between the environment and the organism are not really fully understood. Do environmental conditions, acting on a population for many years, gradually change the genotypic composition of that population, or are individual plants occasionally altered genetically as a result of the direct influence of the environment? Is the action of the environment merely selective? From the work of Turesson and others, and from the writer's own observations on *P. maritima* and species of Gramineae, it is apparent that the local differentiation within a species-population results from the suppression of certain types which are unable to survive in the particular habitat. It is improbable, however, that the eliminating influence of the environment could be wholly responsible for the definiteness of type so often exhibited by local populations (*e.g.* the British freshwater fishes), since it is difficult to imagine what survival value certain characters possess. One is therefore led to assume that, in some cases at least, the partial or even complete isolation which may follow the selective processes of the environment is of considerable importance in establishing the apparently non-essential characters of local populations.

The two populations at present under discussion afford an example of population differentiation unaccompanied by spatial isolation. In nature they occupied two sharply defined, adjoining areas which supported populations of *P. maritima* of different growth habit. The environment had modified both populations considerably, but the effect was more accentuated in the case of the exposed rock plants, the types of which could only be distinguished after a period of transplantation. The progeny of the rock population possessed a larger proportion of low-growing forms than that of the grass population, but the latter contained no

classified type which was not also present in *P* 12 (Table I). The fact that there was a tendency in culture towards a lower habit of growth on the part of the rock population is of significance when it is remembered that the modificatory influences of the wild environment produced a population of dwarfs. There was a decided difference, however, between the cultivated material and that in the wild, since the former exhibited types ranging from the decumbent to the almost erect, whereas in the latter a more or less uniform dwarf population occurred. As Turesson (1922) points out: "the morphological parallelism between the modifications and the hereditary variations offers an additional proof of the control of the environmental factors upon the direction of the differentiation process of the habitat types." Again with reference to Table I, it is apparent that the low growth habit is favoured in the exposed situations and the more upright type in the grass habitat.

Although it is "the sum total of genes which doubtless determine the presence or absence of a certain form in a certain habitat" (Turesson (1922)) it has been suggested (Gregor and Sansome (1927)) that the survival of low-growing forms of *Lolium perenne* L., under conditions of severe grazing, was apparently due to the possession by such plants of a phenotype capable of survival under these conditions. In the case of *P. maritima* it is also possible that occasionally the phenotypical characteristics of growth-forms determine their survival, and one is therefore led to attach some importance to the value of any genotype as represented by a particular phenotype.

Summary.

1. The British distribution of *P. maritima* is continuous throughout the coastal regions, but is localised inland.

2. The species is an aggregate of many growth-forms representing various combinations of characters. Growth habit ranges from the decumbent to the erect form, and five types have been described and figured.

3. Plants derived from a single area on the east coast of Scotland were studied. This locality, though very limited in extent, was ecologically divided into two regions: (*a*) an exposed rock habitat; and (*b*) an adjoining grassy slope.

4. Although the two habitats were not spatially isolated, population differentiation had occurred.

5. In the wild, the environment had modified both populations considerably, but the effect was more marked in the case of the rock population.

6. In culture the rock populations possessed a larger proportion of low-growing forms than did the grass population, but the latter contained no classified type which was not also present in the former.

7. A phenotypic parallelism between the modificatory effect of the environment on the populations in the wild and the growth-forms present in the cultured populations was observed.

8. It is possible that occasionally the phenotypical characteristics of growth-forms determine their survival, and some importance should be attached to the value of the several genotypes represented by a particular phenotype.

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EXPLANATION OF PLATES I, II

Plantago maritima.

Fig. 1. Form I.
Fig. 2. Form II.
Fig. 3. Form III.
Fig. 4. Form IV.
Fig. 5. Form V.
Fig. 6 *a*. Plant *E* 6 collected from the exposed rock habitat. Photo: 17. viii. 26.
Fig. 6 *b*. The same plant in culture. Photo: 3. iv. 28.

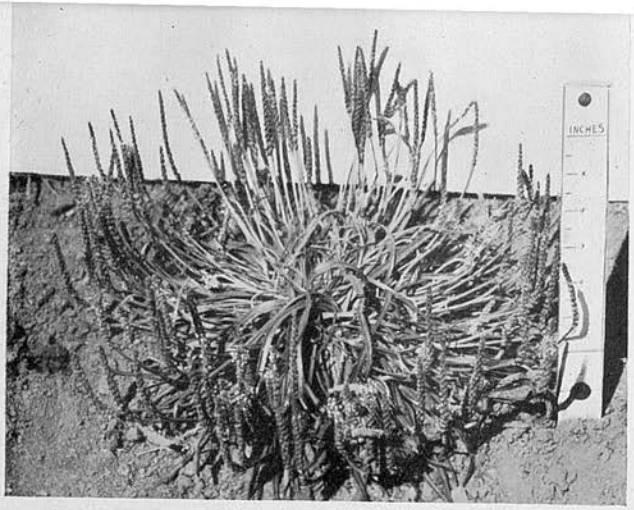
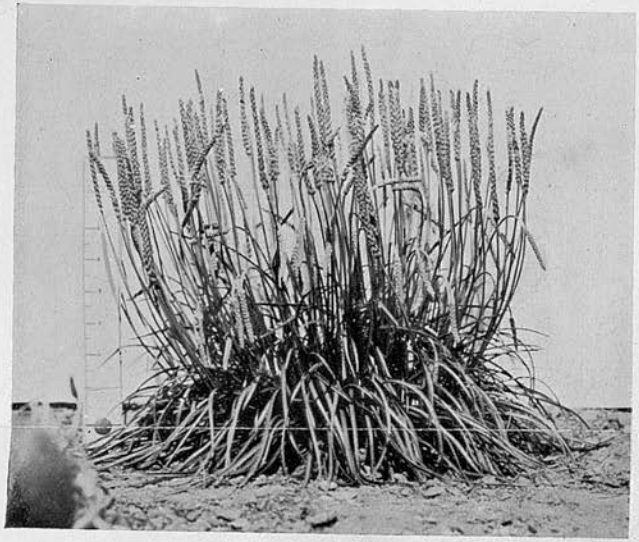


Fig. 1.

Fig. 2.



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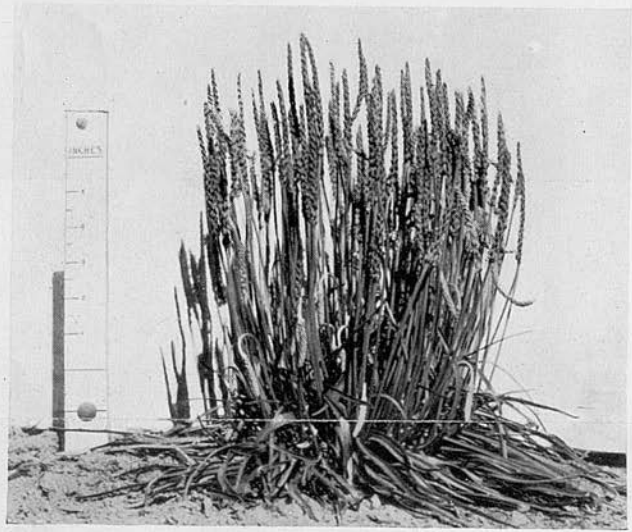

Fig. 4.

Fig. 5.

Fig. 6 (*a*).

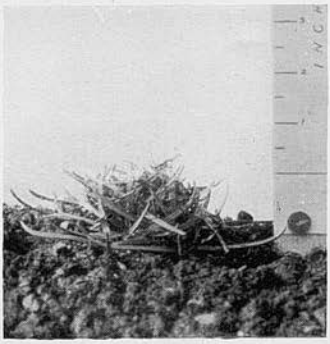

Fig. 6 (*b*).

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EXPERIMENTAL TAXONOMY

I. EXPERIMENTAL GARDEN TECHNIQUE IN RELATION TO THE RECOGNITION OF THE SMALL TAXONOMIC UNITS

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(With 3 figures in the text)

CONTENTS

I. The problem of experimental taxonomy

Experimental studies of plants, both in the field and in the laboratory, have yielded information which appears to various investigators to bear directly on the nature and delimitation of taxonomic units. The classification of organisms on the basis of these experimental facts has been termed *Experimental Taxonomy*. Some doubt may exist as to whether the newer methods may supplant or enrich the existing system of taxonomy, but an examination of the scope of each plainly shows that they should be complementary and mutually helpful. Orthodox taxonomy is concerned with the convenient tabulation of morphological differences; as far as possible the arrangement is natural and it is the only method yet devised that can state to what part of the plant kingdom a dried specimen may belong. Experimental taxonomy fully appreciates the value of

morphological differences—in fact the cytologist has disclosed a fresh field for such investigation—but it also seeks to show the causes which underlie these differences, and to ascertain their physiological, ecological, or genetical nature. The species unit of orthodox taxonomy often includes minor units, which exhibit various degrees of morphological differentiation, regardless of whether such degrees have similar biological significance. Experimental taxonomy, on the other hand, transfers the emphasis from the species unit to the local race (see ecotype concept, Turesson, 1922): it is an attempt to classify evolutionary groups as they occur in Nature. On an extensive scale, as when the flora of a new region is being explored, the existing methods of taxonomy are undoubtedly those that would be employed. Experimental methods, however, would afford a means of probing more deeply into the nature of plant groups such as species of economic importance and others likely to yield valuable data relating to problems of evolution. A system of experimental taxonomy would make readily available this detailed information to botanists studying the phylogeny, distribution and ecology of plants.

Data relative to experimental taxonomy have been accumulating recently, and it has become necessary to consider how they should be documented so as to be available for reference. There are two alternatives: (1) to attempt to incorporate the findings of the experimental taxonomist, perforce relating mainly to the delimitation of the specific and subspecific units, within the framework of the existing system; and (2) to develop a separate but complementary system. Under present conditions the first alternative would add to the existing confusion, for the term species would have to cover not only the *linneon* and the *jordanon* but also some unit established on an experimental basis, e.g. on compatibility, while the smaller experimental units might be indistinguishable in the herbarium. If a complementary system were adopted, at least as a working hypothesis, the results of experimental taxonomic investigations could be coordinated with one another, and since the presentation of the facts could be so arranged as to show the synonymity, if any, between the previous taxonomic names and those of the experimentalist, it should not be difficult to compare the two systems or to employ experimental findings for the clarification of nomenclature if desired. A system has been suggested by Turesson (1922, pp. 344–5; 1929, p. 332; and 1930) which has already been employed in several investigations (Müntzing, 1930, p. 329; Gregor, 1931, p. 212; and Winge, 1933), and which will be adopted in the present studies. Its units are

the *coenospecies*, which has some affinity to Linnaeus's conception of a species, the *ecospecies* and the *ecotype*, and these have their equivalents in the artificially bred economic plants.

The present writers interpret Turesson's classificatory units as follows:

Coenospecies. A group distinguished by morphological, physiological or cytological characters, or a combination of these; separated from all other plants by sterility or by failure of hybrids to produce viable seed. Parts of a coenospecies may have become separated by natural barriers, e.g. oceans or mountain ranges, so that all potential hybridizations cannot occur in Nature.

Ecospecies. A group also distinguished by morphological, physiological or cytological characters, or a combination thereof; separated from other parts of its coenospecies by restricted interfertility or by failure of hybrids to establish themselves in Nature.

Ecotype. A population distinguished by morphological and physiological characters, most frequently of a quantitative nature; interfertile with other ecotypes of the ecospecies, but prevented from freely exchanging genes by ecological barriers. Spatially widely separated ecotypes may exhibit characters determined by genes restricted to the geographical regions in which they occur.

It may be thought that these definitions do nothing more than give yet another meaning to the species, variety and form units of common usage. It seems to the authors, however, that as the categories of experimental taxonomy are to be based on new criteria these should be at least provisionally indicated by the use of appropriate units, rather than that an attempt should be made to modify the meaning of the existing terms to fit the needs of the experimentalist. To illustrate the difficulties arising out of an attempt to reconcile the new treatment with the old terminology three examples may be cited where cytological and ecological differences of importance are not accompanied by striking morphological differences. (1) The species *Pentstemon neotericus* Keck maintains its identity on account of a cytological difference, although it apparently represents a combination of the characters which distinguish two other very closely related species; this difference is associated with an extension of the range of *P. neotericus* into an area unoccupied by either of its two near relatives (Clausen, 1932). (2) *Phleum pratense* L. comprises diploid and hexaploid groups which are practically intersterile and occupy ecologically different habitats (Gregor, 1931). These two groups may correspond to var. *typicum* Beck. and var. *nodosum* (L.)

Richt. and together they probably fall within the sub-species *vulgare* A. & G. (3) In *Vaccinium uliginosum* L., also, polyploidy is followed by a distributional extension, but in this case the two groups have only the status of forms in taxonomic literature. "In general it may be said that the northern limit of the tetraploid form (f. *genuina* Herd.) lies slightly more to the north than the southern limit of the diploid form (f. *microphylla* Lange). Only in those regions (round the polar circle) can these two forms be found together, the diploid form being of a more markedly arctic distribution than the tetraploid" (Hagerup, 1933, p. 127). From these examples it can be seen that units of similar biological significance have been given the varying status of species, varieties and forms.

The principles of an experimental taxonomic investigation as at present conceived may be stated thus: (1) choice of a group of plants; (2) collection of samples over its geographical and ecological ranges; (3) cultivation of representative samples in an experimental garden; (4) observation of discontinuous, and biometrical comparison of continuous variations; (5) study of fertility relationships; (6) investigation of cytology; and (7) synthesis of results. In the present paper the first four operations are dealt with. Although the experiments described are mainly exploratory and have special reference to the sea plantains, the practical methods devised should be of use in other studies along similar lines. One of the fundamental features of this experimental attack is the substitution for the natural habitat, with its all too frequent irregularities, both physical and biotic, of an artificial and, as far as possible, a controlled environment in the form of a specially prepared experimental garden, where the polymorphy and characters of races can be studied under uniform conditions, and statistical methods applied. Character differences which have been accurately evaluated under these circumstances should reflect true hereditary dissimilarity. At the same time the experimentalist has the opportunity of thoroughly examining racial fertility relationships. The determination of the restrictions imposed upon the free diffusion of genes in Nature by sterility and other factors is a matter of very considerable taxonomic importance. Moreover, as sterility relationships have a bearing on genetical relationships, the simultaneous investigation of both is advantageous (for a discussion of these see Müntzing, 1930, pp. 314–30, and for genetical analytical methods see Matsuura, 1935, p. 145).

Experimental taxonomy should seek, therefore, to develop a method of classification which would take into consideration not only

the magnitude of the morphological and physiological differences of its units, but also the causes which maintain their identity, e.g. isolation in its various forms. But classificatory categories based primarily on such restrictions to gene exchange will, as in systems where other criteria are employed, inevitably lose their significant status if the dynamic nature of their components is not fully appreciated. Furthermore, if the system is to present successfully the results of experimental investigation, it will require to be sufficiently flexible to meet the needs of investigators working with divers kinds of material, and to provide a framework for future taxonomic development.

II. Methods of sampling populations

Material

The investigations in progress at this institute embrace an experimental study of the sea plantains (*Plantago maritima* L. and allied species) of Europe and North America. The present paper, the first of a series, deals with methods of sampling habitat populations, and their examination under experimental conditions. In succeeding papers it is hoped to deal with such aspects as character correlations, the races occurring in Britain, and the interrelationships of the North European and North American sea plantains.

This plant was chosen for the investigations because of its suitability as experimental material, since its various characters lend themselves comparatively readily to statistical measurements. The populations studied were characterized, not so much by their possessing peculiar constituents, as by the differing proportions in which the various types occurred. It was probably the size characters and those characters which together make up growth habit which most obviously distinguished one population from another. Size, however, while ecologically important, is one of the many quantitative characters which does not lend itself to verbal treatment, and which, moreover, cannot be studied with accuracy in the wild.

Collection of material

In preliminary experiments, plants were transferred from the natural habitats to the garden, but for several reasons, e.g. the difficulty of distinguishing age groups in the wild and of transporting plants alive over long distances, this method was discontinued in favour of the taking of seed samples. In collecting seed samples, ripe spikes were systematically gathered from comparatively well-defined

but not necessarily spatially isolated habitats, the number of spikes per plant collected from any one habitat depending on the density of the plantain population.

Cultivation of material

Each seed sample was sown in a heated glasshouse (60° F.), in a pan containing sterilized weed-free soil, during late February, the seedlings being later transferred to boxes placed in a cool house. In June they were transplanted to their positions in the experimental garden. The garden (Fig. 1) was planned so that each year one-third

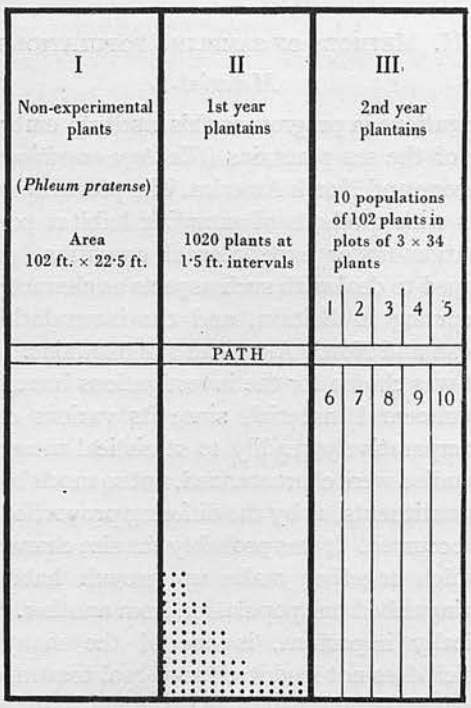

Fig. 1. Experimental garden.

of its area contained one-year-old plantains, one-third two-year-old plantains, and one-third a non-experimental crop. Ten populations could be examined each year, either systematically arranged as plots of 102 plants in three rows of thirty-four, or as six rows of seventeen plants distributed at random. The history of each section was as follows. The young plantains planted out in June were generally not observed during the first summer. They survived the winter and

became the experimental material of the second summer, at the end of which they were discarded and *carted off*. A definite amount of well-rotted farmyard manure was then applied to the vacated section and in the spring *Phleum* plants were grown; in the autumn these also were carted off. By this treatment about 18 months elapsed between the removal of one crop of plantains and the introduction of the next, thus giving time for cleaning and for the manure to mix thoroughly with the soil.

Characters and statistics

Every plant received a number and the data relating to each were systematically recorded. The samples for laboratory examination were collected in numbered specimen tubes contained in a carrier. A description of the characters studied is given below. Owing to limitations of space, it has been found necessary in the tables to utilize abbreviations of which the following is a list:

A, anther.	**H**, height.	**Sc**, scape.
AT, anther tip.	**HbG**, habit grade.	**Sd**, seed.
B, breadth.	**Ix**, index.	**Sep**, sepal.
Br, bract.	**L**, length.	**Sp**, spike.
D, density.	**Lf**, leaf.	**Th**, thickness.
FlG, flowering grade.	**S**, spread.	

Examples: **LfL** = leaf length, **AL** = anther length, **BrB** = bract breadth, etc.

Size of organs.

LfL and **LfB** (mature characters). The largest leaf on each plant is chosen by eye (28 July). Its length is measured in cm. and its maximum breadth in mm.

ScL and **SpL** (mature characters). The longest scape on each plant is chosen by eye and is pulled, not cut (25 July). Scape length includes rachis, spike length extends from the lowest floret to the apex; both are measured in cm.

LfTh and **ScTh**. Measured correct to 0·1 mm. with a micrometer screw gauge. Leaf thickness is taken at the midpoint on the midrib of the longest leaf (5 May). Scape thickness at the midpoint of the longest scape (25 July).

The following characters are measured by arranging the organs in rows on a slide smeared with glycerine and using a microscope with

a movable stage. The micrometer units, each of which is equivalent to 0·04286 mm., have been retained in this paper.

BrL, BrB, SepL and **SepB**. A mature spike, not one of the earliest to flower, is chosen, and from the midpoint a bract is removed. The abaxial sepal underlying this bract and to its left relative to the dorsal aspect is also detached, and both are placed, convex side uppermost, on the slide. Lengths are measured from apex to base; breadths across the widest point, that of the bract including the membranous margins.

AL and **ATL**. An anther is detached from a flower at the mid-point of a spike after exsertion and before dehiscence, and placed with filament uppermost on the slide. Anther length is the total length including subulate tip, anther tip length is the length of the tip from apex to the level of the anther lobes.

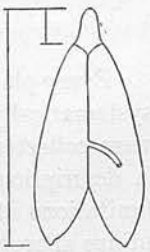

Fig. 2.

SdL and **SdB**. From a ripe capsule containing two well-developed seeds the larger is chosen. This is placed on the slide convex surface uppermost. Both length, and breadth at the widest point, are measured exclusive of membranous margins.

Size of plants.

LfS, LfH, ScS and **ScH**. Spread is taken as the distance in inches between the apices of the longest leaves, or longest scapes, at opposite points in the perimeter of the plant. Height is measured from ground-level to the highest point of the leaf or scape system, half inches being the grouping units for leaf, and inches for scape. The leaves are measured prior to exsertion of spikes (5 May), the scapes at maturity (14 July).

Arrangement of flowers.

SpD. A numerical expression of the density of spike. The number of flowers, or parts thereof, attached to the middle cm. cut with a razor from a spike which is mature but not one of the earliest.

Indices and other ratios.

BrIx, SepIx and **SdIx**. These three ratios, which indicate the shapes of the respective organs, are calculated for each plant from the data of length and breadth.

BrL : SepL, ScL : SpL, ScL : LfL. These ratios are calculated for each plant from the specified measurements. They represent certain

relationships between size of parts which have been employed in taxonomic description.

Estimates of habit and time of flowering.

LfS : H and **ScS : H.** Ratios indicating growth habits of leaf and scape systems.

HbG. An arbitrary estimate of habit, giving somewhat more information than the scape ratio. It consists of five grades ranging from decumbent to erect. In grade 1 spikes are restricted to the periphery, in the other four they are evenly distributed.

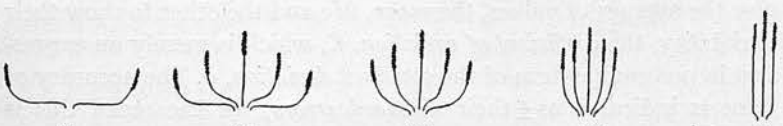

Fig. 3.

This "character" is dependent on the observer, though controlled by reference to standard photographs (Gregor, 1930, Pl. I and II). Owing to the small number of classes, it is the least satisfactory for statistical studies.

FlG. In order to obtain statistical data of time of flowering, each plant is classed as being at one of the following eleven stages:

(1) Spikes not yet visible.
(2) Spikes just visible.
(3) Spikes easily visible.
(4) Spikes well developed.
(5) Stigmas of lower flowers visible.
(6) Plants beginning to flower; up to approximately 12 per cent of spikes flowering.
(7) Plants flowering sparsely; approximately 25 per cent of spikes flowering.
(8) Plants flowering freely; approximately 50 per cent of spikes flowering.
(9) Plants flowering abundantly; approximately 75 per cent of spikes flowering.
(10) Spikes fading; approximately 12 per cent of spikes completed flowering.
(11) Spikes much faded; approximately 25 per cent of spikes completed flowering.

Such a classification is, of course, dependent on the judgement of the observer, but the grades provide a relative order of flowering, the higher variates being the earlier. Observations are made on three

occasions, 1, 8 and 28 June. The first and last generally show skew distributions, while those of the middle date are more symmetric and afford the best picture of relative maturity.

Although some of the size characters examined showed curves with somewhat skew tails in the higher range they all seemed sufficiently unimodal to receive normal statistics. In fact the majority of the characters studied, including all those defined above, proved amenable to statistical treatment. In the cases where such methods were rejected it was on account of unsuitable frequency distributions.

For describing populations two main statistics are used, one to give the average of values, the *mean*, M; and the other to show their variability, the *coefficient of variation*, C, which is merely an expression in percentage form of the *standard deviation*, σ. The accuracy of these is indicated as $\pm$ their *standard errors*; for the mean this is $\sigma/\sqrt{n}$, where n is the number of observations (Fisher, 1932, p. 48); while for C it can be found from Pearson (1914, p. xxii). The *significance* of a difference between a pair of M or C values can be expressed as D/E_d, or the ratio of *difference: error of difference* (where $E_d = \sqrt{E_1^2 + E_2^2}$); the odds against D/E_d exceeding 2·58 by accident are 100 : 1, so that >3 can be taken as a convenient measure of significance. Two types of correlation are used for special purposes in Tables III and IV, both having the coefficient r (see Fisher, 1932, *interclass* Chap. VI, *intraclass* p. 193). The methods applicable to uniformity trials and for dealing with populations in randomized plots, in so far as they have reference to the present paper, may be found in Fisher (1932, pp. 242 *et seq.*), or in Fisher & Wishart (1930).

III. RELIABILITY OF SAMPLING METHODS

Single plant sampling

The experiments of which the results are summarized in Tables I and II were designed to ascertain the validity of the methods of sampling described above for the various characters. In order to find out how the variability within a single plant compares with that of the whole population, the entire complement of certain organs of a few individual plants was measured. From Table I it will be seen that the variability of these organs equals or even exceeds that of the whole population; which indicates that reliable data concerning populations cannot be obtained by random sampling of their constituent plants. Table II shows that even parts on the same organ, e.g. bracts and sepals on the same spike, have a variability compar-

TABLE I. *Coefficients of variation for individual plants and parent populations*

	Population PMN 44			PMN 54 (*a*)		PMN 81		PMN 84	
Character	Plant A	Population	Plant B	Plant	Population	Plant	Population	Plant	Population
ScL	11·50 ± ·684	12·96 ± ·932	10·80 ± ·474	13·91 ± ·778	11·42 ± ·818	6·81 ± ·477	13·45 ± 1·294	8·82 ± ·478	14·32 ± 1·043
SpL	23·31 ± 1·442	21·41 ± 1·582	24·30 ± 1·113	33·70 ± 2·048	17·42 ± 1·268	15·60 ± 1·118	17·58 ± 1·714	22·85 ± 1·302	19·19 ± 1·420
BrL	13·40 ± ·801	11·62 ± ·837	12·10 ± ·532	30·62 ± 1·832	12·38 ± ·884	10·94 ± ·775	8·33 ± ·788	10·08 ± ·552	10·19 ± ·747
BrB	13·44 ± ·803	11·91 ± ·858	14·53 ± ·643	15·32 ± ·860	9·54 ± ·672	9·03 ± ·632	8·85 ± ·836	10·74 ± ·589	8·90 ± ·646
BrIx	6·71 ± ·394	13·70 ± ·992	6·75 ± ·293	15·92 ± ·896	9·80 ± ·690	6·77 ± ·474	7·58 ± ·716	6·62 ± ·359	7·74 ± ·562
SepL	5·93 ± ·348	7·34 ± ·521	4·64 ± ·201	10·18 ± ·564	6·77 ± ·476	6·21 ± ·435	5·84 ± ·552	7·68 ± ·416	10·87 ± ·798
SepB	6·26 ± ·368	10·26 ± ·737	8·55 ± ·371	7·70 ± ·423	7·77 ± ·547	5·37 ± ·376	6·22 ± ·587	9·02 ± ·489	10·08 ± ·739
SepIx	7·22 ± ·424	11·42 ± ·822	7·20 ± ·312	6·02 ± ·331	8·66 ± ·609	5·77 ± ·404	7·87 ± ·744	7·69 ± ·417	10·42 ± ·765
BrL : SepL	11·08 ± ·658	10·53 ± ·757	9·75 ± ·423	20·74 ± 1·186	9·85 ± ·693	7·02 ± ·491	8·90 ± ·842	7·44 ± ·403	7·97 ± ·578
Mean	10·98	12·35	10·96	17·12	10·40	8·17	9·40	10·10	11·08

TABLE II. *Data from individual spikes of PMN 54 plant* (27)

	Early-flowering spike				Later-flowering spike			
Character	Lower 1/3	Middle 1/3	Upper 1/3	Entire spike	Lower 1/3	Middle 1/3	Upper 1/3	Entire spike
				Mean values				
BrL	104·37 ± ·870	88·08 ± 1·406	63·66 ± ·555	85·08 ± 1·522	81·84 ± ·551	73·68 ± ·481	61·05 ± ·823	72·45 ± ·794
BrB	44·72 ± ·495	39·87 ± ·268	37·14 ± ·340	40·53 ± ·341	38·64 ± ·472	36·83 ± ·250	35·00 ± ·403	36·87 ± ·257
SepL	69·96 ± ·213	68·34 ± ·198	63·37 ± ·310	67·17 ± ·276	67·02 ± ·307	65·96 ± ·191	61·89 ± ·249	64·99 ± ·235
SepB	35·64 ± ·290	36·57 ± ·283	34·14 ± ·239	35·43 ± ·177	34·42 ± ·228	34·60 ± ·199	32·94 ± ·199	34·35 ± ·147
BrL : SepL	1·49 ± ·014	1·29 ± ·019	1·00 ± ·005	1·26 ± ·019	1·22 ± ·010	1·12 ± ·007	0·98 ± ·012	1·11 ± ·010
BrIx	2·35 ± ·026	2·21 ± ·030	1·73 ± ·016	2·09 ± ·027	2·13 ± ·021	2·00 ± ·019	1·74 ± ·016	1·96 ± ·017
SepIx	1·97 ± ·020	1·87 ± ·017	1·86 ± ·012	1·90 ± ·010	1·89 ± ·014	1·91 ± ·012	1·88 ± ·012	1·89 ± ·007
				Coefficients of variation				
BrL	5·72 ± ·590	10·95 ± 1·143	6·12 ± ·617	21·39 ± 1·425	4·90 ± ·475	4·52 ± ·462	9·44 ± ·954	13·42 ± ·789
BrB	7·59 ± ·783	4·61 ± ·475	6·41 ± ·648	10·07 ± ·649	8·89 ± ·864	4·70 ± ·479	8·06 ± ·814	8·54 ± ·493
SepL	2·09 ± ·215	1·99 ± ·205	3·42 ± ·346	4·91 ± ·313	3·33 ± ·323	2·00 ± ·204	2·82 ± ·285	4·42 ± ·255
SepB	5·57 ± ·575	5·31 ± ·548	4·90 ± ·495	5·96 ± ·380	4·69 ± ·455	3·99 ± ·407	4·22 ± ·427	5·26 ± ·304
BrL : SepL	6·57 ± ·678	10·02 ± 1·044	3·72 ± ·376	17·76 ± 1·168	6·07 ± ·589	4·45 ± ·454	8·33 ± ·842	10·93 ± ·639
BrIx	7·59 ± ·783	9·39 ± ·969	6·56 ± ·663	15·22 ± ·993	7·14 ± ·694	6·39 ± ·653	6·53 ± ·659	10·63 ± ·621
SepIx	6·88 ± ·710	6·33 ± ·653	4·64 ± ·469	6·52 ± ·416	5·46 ± ·530	4·17 ± ·425	4·30 ± ·434	4·71 ± ·272

able with that of the whole plant or even of the population. It is shown, moreover, that the variability of these parts is greater on the earliest spikes than on later ones, and that the region of least variability is the middle third of the later flowering spikes (cf. p. 330). It might be thought that the best method of estimating the mean value for a character throughout a population would be to calculate the mean of each plant for that character, as in Table I, or at least to base this calculation on as large a sample from each plant as possible. There are, however, certain obvious practical objections to such a method, for it would be extremely laborious and might seriously damage the plants. Apart, however, from these objections the method itself is open to criticism. For example, two equally long-leaved plants might easily be found to have different mean values for leaf length if one of them possessed a greater proportion of immature leaves at the time of examination.

It will be seen, then, that for the examination of populations comprising many plants it is a practical necessity to reduce the number of samples per plant to an absolute minimum, that is to one, if it can be ascertained that such a procedure is consistent with accuracy. It is necessary, therefore, to substitute *selective* for *random* sampling in order to obtain specimens that may be regarded as equivalent to one another. Pearson (1901) showed that by selecting organs of like maturity and similar position on the plant he obtained comparable specimens upon which to measure characters. These he termed *homotypes*, and he showed, by means of intraclass correlations on vast quantities of material, that homotypes within a plant are strongly correlated, or much more alike than are homotypes of different plants of a habitat population. Some small tests of this nature have been made on the validity of certain characters, advantage being taken of Harris's short method of calculation (Fisher, 1932, p. 193). It facilitates the work of recording if several characters can be measured on a selected organ. For example the longest leaf and scape, which are homotypes readily distinguishable by eye, are chosen for measurements of length, breadth and thickness; while for bract and sepal measurements a floret is taken from the midpoint of a mature and somewhat late flowering spike, thus limiting the sampling to the region of least variability on a spike with comparatively low variability (see Table II). Selective methods for other characters have been noted in the descriptions (pp. 329–30).

From each of 102 plants, quintuplicate selections were made, i.e. the five longest leaves and scapes, and five spikes for measurements of

sepals, bracts and spike density. Ten anthers were taken from each of fifty-four plants since there was difficulty in finding 102 plants in flower at the same time. In Table III the likeness of characters may be most readily seen from the intraclass correlation coefficients, where +1·0 would imply that they were identical. An alternative method of expression is the comparison of "variances" ($=\sigma^2$), upon which Fisher's z test of significance can be applied. It will be seen

TABLE III. *Intraclass correlation to test validity of homotypes*

PMN 44. 102 plants, 5 homotypes. Anthers 54 plants, 10 homotypes.

Character	Coefficient of correlation	Variance: Between plants	Variance: Within plants	z	$\frac{\text{S.E.}_{\cdot 100}}{M} \times 100$
				$(n_1=101)$ $(n_2=408)$	
LfL (5 May)	+·959	78·91	0·623	2·42	0·404
LfB (5 May)	+·738	12·36	0·802	1·37	1·323
LfTh (5 May)	+·657	0·042	0·0039	1·19	0·656
LfL (28 July)	+·930	93·17	1·319	2·13	0·408
LfB (28 July)	+·919	19·60	0·326	2·05	0·786
SpL	+·729	24·90	1·691	1·35	1·305
ScL	+·948	161·50	1·645	2·29	0·318
ScTh	+·930	0·341	0·0048	2·13	0·380
BrL	+·853	52·23	1·703	1·71	0·587
BrB	+·746	49·06	3·064	1·39	0·606
BrIx	+·847	0·396	0·0120	1·69	0·473
SepL	+·934	13·96	0·186	2·16	0·228
SepB	+·685	27·97	2·319	1·25	0·598
SepIx	+·688	0·278	0·0227	1·25	0·671
SpD	+·737	22·13	1·446	1·36 $(n_1=53)$ $(n_2=486)$	0·914
AL	+·856	196·98	3·158	2·07	0·350
ATL	+·828	20·57	0·405	1·96	0·970

that the correlations range from +0·96 to +0·66, and that there is no question as to their significance. As length is the criterion in choosing scape and leaf it is gratifying to find high uniformity among the five longest. Other characters measured on these organs show more variability, especially leaf thickness. Variance within plants is now much smaller than between plants (cf. Table I), while the standard error for 100 observations, expressed as a percentage of their mean, affords some idea of the extent of errors due to sampling a population, for it exceeds 1 per cent in only two cases.

When some studies (unpublished) were being made on the ordinary correlations between characters (interclass), a special question of sampling arose, as to what difference there might be in using pairs of measurements made on one organ as opposed to pairs on two similar organs of a plant. Pearson (1901) has explored this question and shown that interclass correlations of characters on the

same organ, which he called *organic*, gave somewhat higher values than those on different organs (*cross-homotypic*). Interclass correlations of these kinds have been calculated to ascertain to what extent such discrepancies might affect the plantain studies. Employing data gathered for Table III, records of the characters of four homotypes from each of 102 plants afforded 408 pairs for correlation, while in the case of anthers, ten homotypes on fifty-four plants gave 540 pairs. Correlating length with breadth of leaf for example, the *organic* coefficient was calculated from 408 pairs of measurements, each pair on a single leaf; while to obtain the *cross-homotypic* coefficient the length of leaf 1 was coupled with the breadth of leaf 2, and vice versa, the same being done with leaves 3 and 4 in each plant, so that 408 pairs were again utilized. In Table IV it will be seen that the organic coefficients (below and to the left of the diagonal) are somewhat

TABLE IV. *Comparison of organic with cross-homotypic correlations* (*PMN* 44)

5 May	Cross homotypic LfL	LfB	LfTh		Cross-homotypic SpL	ScL	ScTh
LfL	—	+·444	+·201	SpL	—	+·725	+·678
LfB	+·456	—	+·197	ScL	+·734	—	+·587
LfTh	+·218	+·196	—	ScTh	+·719	+·596	—
	Organic				Organic		

28 July	LfL	Organic	+·252	AL	Organic		−·132
	LfB	Cross-homotypic	+·242	ATL	Cross-homotypic		−·150

Character	Cross-homotypic BrL	BrB	BrIx	SepL	SepB	SepIx	SpD
BrL	—	+·523	+·577	+·620	+·270	+·226	−·232
BrB	+·628	—	−·072	+·439	+·427	−·064	−·283
BrIx	+·649	−·167	—	+·360	−·071	+·347	−·029
SepL	+·655	+·463	+·383	—	+·315	+·387	−·261
SepB	+·304	+·488	−·094	+·318	—	−·469	−·113
SepIx	+·228	−·096	+·388	+·442	−·671	—	−·089
SpD	−·286	−·331	−·020	−·265	−·169	−·043	—
		Organic					

greater than the cross-homotypic values (above and to the right). This applies to both positive and negative correlations, with three or four exceptions in all of which the coefficients are insignificant. The magnitude of differences is generally small, averaging about 0·03, but occasionally exceeding 0·1, and it seems to depend on the strength of correlation in conjunction with variability of the homotypes within the plant (contrast behaviour in scape and bract groups). It was decided that organic characters should be used for the studies in question, because there is less likelihood of errors due to sampling.

To avoid confusion a brief restatement may be made: (1) characters on different organs of a plant, e.g. on the leaves, vary enormously; (2) random sampling would give a very imperfect idea of the plant; (3) some form of selective sampling is needed, (4) this is achieved by selecting organs that are apparently equivalent (homotypic), such as the longest leaf, scape, etc.; (5) a statistical test (Table III) shows that the methods of sampling appear to be justified, although all characters are not equally satisfactory; (6) ratios such as bract length : breadth should naturally be measured on the same organs, and when correlation studies are contemplated it seems advisable (Table IV) to measure as many characters as possible on the same organ.

Influence of season on population data

(*a*) *Within years.* The examination of replicate samples of the same population in the same season afforded a guide to the reliability attainable by the adopted sampling technique. In Table V (A and B) are shown the mean values for various characters for duplicate samples of populations PMN 18 and PMN 20 examined in the same year. With the exception of the values for leaf and scape thickness in PMN 18, no mean difference exceeds twice its standard error, showing that such differences as do occur can safely be regarded as insignificant. An estimate of the magnitude of the mean differences, in percentage form, is given for comparative purposes. In Table V (C) two closely related populations PMN 21 and PMN 44 are compared. These were collected from the same habitat in the same year, but by different methods. PMN 21 was derived from a seed sample collected in the manner already described (p. 327), while PMN 44 was raised from a sample of plants transferred from the wild and seeded in isolation at Edinburgh. As in the duplicated samples of PMN 18 and PMN 20 the differences between the character mean values fail to reach the significant level. In contrast with the above the mean values for two different habitat populations (Table V (D)) exhibit differences which are unquestionably significant, that of the scape height means being as great as 44·8 times its error. These data show that when populations are compared in the same year and at the same place the accuracy of the technique is sufficient to ensure the detection of real differences in population characteristics.

In 1930 samples of two populations, PMN 21 and PMN 32, were grown from seed at Edinburgh. One 102-plant sample of each was transplanted into the experimental garden at this institute on 30 June,

and duplicate samples were sent to Dr W. B. Turrill at Kew, Surrey, and transplanted into the garden there on 3 July. Records of time of flowering and plant height were made in the following season

TABLE V. *Reliability of within-year data from* 100*-plant plots*

	A. Duplicate plots of PMN 18				B. Duplicate plots of PMN 20			
Character	(*a*) M	(*b*) M	$\frac{D \times 100}{M}$	$\frac{D}{E_d}$	(*a*) M	(*b*) M	$\frac{D \times 100}{M}$	$\frac{D}{E_d}$
LfL	27·95±·492	27·35±·551	2·17	0·81	22·26±·500	20·94±·474	6·11	1·92
LfB	6·77±·183	7·01±·169	3·48	0·96	5·44±·162	5·48±·168	0·73	0·17
LfTh	1·01±·016	1·11±·017	9·43	4·22	1·18±·017	1·19±·016	0·84	0·43
ScL	36·30±·552	36·40±·493	0·28	0·14	33·04±·723	31·65±·619	4·30	1·46
ScTh	1·94±·023	1·81±·022	6·93	4·10	2·10±·027	2·05±·027	2·41	1·32
SpL	9·75±·180	9·71±·163	0·41	0·17	10·06±·218	10·14±·243	0·79	0·25
LfS	9·14±·234	9·58±·214	4·70	1·39	10·10±·249	9·44±·247	6·76	1·88
LfH	3·59±·121	3·75±·106	4·36	0·99	2·85±·083	2·62±·086	8·41	1·93
ScS	18·20±·330	17·61±·309	3·30	1·32	17·02±·274	16·37±·286	3·89	1·64
ScH	14·26±·254	14·43±·243	1·19	0·48	11·62±·300	11·15±·300	4·13	1·11
LfS : H	2·62±·067	2·58±·053	1·54	0·47	3·62±·165	3·61±·170	0·28	0·04
ScS : H	1·27±·023	1·25±·020	1·59	0·66	1·54±·032	1·57±·047	1·45	0·52

	C. Related populations				D. Different habitat populations			
	PMN 21 M	PMN 44 M	$\frac{D \times 100}{M}$	$\frac{D}{E_d}$	PMN 32 M	PMN 42 M	$\frac{D \times 100}{M}$	$\frac{D}{E_d}$
LfL	27·21±·530	27·28±·418	0·26	0·10	15·82±·522	36·01±·678	77·91	23·60
LfB	6·02±·154	6·06±·136	0·66	0·20	4·14±·181	10·83±·174	89·38	26·64
LfTh	1·08±·015	1·10±·014	1·83	0·99	1·02±·018	1·24±·021	19·47	8·04
ScL	38·59±·584	38·49±·422	0·26	0·14	22·09±·538	51·93±·595	80·63	37·21
ScTh	1·70±·027	1·78±·024	4·60	2·23	1·72±·029	2·01±·022	15·55	8·03
SpL	9·15±·219	9·78±·175	6·66	2·25	6·62±·181	9·46±·196	35·32	10·64
LfS	13·89±·291	14·51±·238	3·72	1·38	6·08±·219	18·21±·271	99·88	34·80
LfH	4·27±·121	4·47±·112	4·58	1·23	1·81±·073	7·41±·151	121·48	33·45
ScS	19·45±·377	19·80±·258	1·78	0·77	13·06±·312	20·04±·396	42·18	13·84
ScH	15·39±·270	15·60±·183	1·36	0·61	7·06±·227	22·40±·257	104·14	44·79
LfS : H	3·42±·083	3·42±·070	0·00	0·00	3·51±·098	2·52±·043	32·84	9·26
ScS : H	1·29±·030	1·29±·017	0·00	0·00	1·98±·056	0·90±·015	75·00	18·80

simultaneously at each centre. The results are given in Table VI. The order both of flowering and height of plants remained unchanged at both localities, but the late-flowering low-growing population, PMN 32, responded more to the changed environment than did PMN 21.

TABLE VI. *Mean values for flowering grade and scape height at two centres*

Population	PMN 21		PMN 32	
Character	FlG	ScH	FlG	ScH
Edinburgh	3·49±·132	15·39±·270	2·43±·146	7·06±·227
Kew	2·95±·141	15·72±·221	1·29±·075	9·30±·281
$\frac{M'-M''}{M} \times 100$	16·77	2·12	61·29	27·38
$\frac{\text{Difference}}{\text{Error of } D}$	2·798	0·946	6·960	6·202

The populations, however, tended to be later flowering and larger at Kew, significantly so in the case of PMN 32. The coefficients of variation, nevertheless, remained similar in both environments, e.g., for plant height the coefficients of variation for PMN 21 were 17·73 per cent ± 1·280 at Edinburgh and 14·01 per cent ± 0·964 at Kew, and the corresponding values for PMN 32 were 32·25 per cent ± 2·482 and 30·21 per cent ± 3·325.

(*b*) *Between years*. When samples of the same population were examined in four different years, the differences between the extreme yearly means of the majority of characters exceeded three times their respective errors (Table VII); the corresponding coefficients of varia-

TABLE VII. *Reliability of mean values of different years* (*PMN* 44)

Character	Mean values				General mean	Greatest diff. × 100 / Gen. mean	Greatest diff. / Error of *D*
	1931	1933	1934	1935			
LfL	27·28 ± ·418	27·71 ± ·440	27·50 ± ·462	26·80 ± ·409	27·32	3·33	1·52
LfB	6·06 ± ·136	7·02 ± ·176	7·00 ± ·160	7·32 ± ·171	6·85	18·39	5·76
LfTh	1·10 ± ·014	0·87 ± ·016	0·79 ± ·012	0·94 ± ·011	0·93	33·33	17·08
ScL	38·49 ± ·422	41·15 ± ·464	40·70 ± ·527	41·57 ± ·498	40·48	7·61	4·72
ScTh	1·78 ± ·024	1·60 ± ·024	1·63 ± ·023	1·87 ± ·021	1·72	15·70	8·51
SpL	9·78 ± ·175	9·99 ± ·202	9·80 ± ·210	10·22 ± ·182	9·95	4·52	1·74
SpD	13·36 ± ·177	13·65 ± ·219	13·12 ± ·197	12·91 ± ·225	13·26	5·58	2·36
BrL	64·33 ± ·910	60·65 ± ·862	65·00 ± ·759	67·00 ± ·983	64·25	9·88	4·86
BrB	29·07 ± ·313	26·80 ± ·321	29·00 ± ·347	29·07 ± ·367	28·49	7·97	4·66
BrIx	2·25 ± ·030	2·27 ± ·028	2·26 ± ·031	2·31 ± ·029	2·27	2·64	1·44
SepL	—	57·20 ± ·558	57·33 ± ·423	56·59 ± ·503	57·04	1·30	1·13
SepB	—	24·64 ± ·274	24·86 ± ·256	25·60 ± ·245	25·03	3·84	2·61
SepIx	—	2·35 ± ·028	2·32 ± ·027	2·23 ± ·026	2·30	5·22	3·13
SdL	53·30 ± ·352	57·28 ± ·369	55·91 ± ·399	57·29 ± ·363	55·95	7·13	7·89
SdB	23·13 ± ·135	23·82 ± ·129	23·88 ± ·143	23·64 ± ·171	23·62	3·18	3·82
SdIx	2·30 ± ·014	2·42 ± ·018	2·35 ± ·016	2·43 ± ·017	2·38	5·46	5·93
AL	47·30 ± ·627	44·60 ± ·391	46·39 ± ·361	46·08 ± ·367	46·09	5·86	3·66
ATL	6·76 ± ·211	6·59 ± ·123	6·23 ± ·097	6·34 ± ·114	6·48	8·18	2·29
FlG	3·86 ± ·117	5·06 ± ·154	3·98 ± ·137	3·73 ± ·106	4·16	31·97	7·11
LfS	14·51 ± ·238	16·11 ± ·279	14·26 ± ·237	15·42 ± ·278	15·08	12·28	5·49
LfH	4·47 ± ·112	4·46 ± ·105	5·41 ± ·124	4·89 ± ·128	4·81	19·71	5·84
ScS	19·80 ± ·258	20·67 ± ·269	21·33 ± ·274	19·22 ± ·263	20·25	10·41	5·10
ScH	15·60 ± ·183	16·59 ± ·189	16·62 ± ·241	16·62 ± ·220	16·36	6·23	3·37
LfS : H	3·42 ± ·070	3·80 ± ·097	2·74 ± ·062	3·30 ± ·074	3·31	32·02	9·21
ScS : H	1·29 ± ·017	1·26 ± ·018	1·31 ± ·019	1·18 ± ·017	1·26	10·32	5·04
HbG	2·43 ± ·053	2·92 ± ·073	2·84 ± ·061	2·89 ± ·064	2·77	17·69	5·91
BrL : SepL	—	1·06 ± ·010	1·13 ± ·012	1·18 ± ·015	1·12	10·71	6·69
ScL : SpL	—	4·25 ± ·072	4·30 ± ·072	4·18 ± ·067	4·24	2·83	1·22
ScL : LfL	—	1·51 ± ·020	1·51 ± ·020	1·59 ± ·017	1·54	5·19	3·09

tion on the other hand showed less fluctuation (Table VIII). From Table VII it will be seen that the leaf characters, with the exception of length, vary markedly from year to year. Leaf spread, height and

thickness, being immature characters, fluctuate according to whether spring growth is late or early; they naturally are liable to greater seasonal fluctuations than leaf length, which is a mature character.

TABLE VIII. *Reliability of coefficients of variation between years* (*PMN* 44)

Character	Coefficients of variation (%) 1931	1933	1934	1935	General mean	Greatest diff. × 100 / Gen. mean	Greatest diff. / Error of *D*
LfL	17·87±1·12	15·86±1·15	16·79±1·22	15·34±1·11	16·47	15·36	1·604
LfB	25·90±1·68	25·08±1·88	22·86±1·70	23·55±1·75	24·35	12·48	1·272
LfTh	13·91±0·86	18·45±1·34	15·09±1·09	12·22±0·87	14·92	41·76	3·899
ScL	12·87±0·79	11·27±0·81	12·96±0·93	11·97±0·86	12·27	13·77	1·371
ScTh	15·55±0·97	14·78±1·07	14·36±1·04	11·29±0·81	14·00	30·43	3·370
SpL	20·82±1·32	20·25±1·49	21·41±1·58	17·80±1·30	20·07	17·99	1·764
SpD	13·28±0·95	16·06±1·17	14·98±1·08	17·56±1·27	15·47	27·67	2·699
BrL	14·00±1·00	14·20±1·02	11·62±0·84	14·82±1·06	13·66	23·43	2·366
BrB	10·79±0·77	11·96±0·86	11·91±0·86	12·77±0·91	11·86	16·69	1·661
BrIx	13·04±0·93	12·41±0·89	13·70±0·99	12·96±0·90	13·03	9·90	0·969
SepL	—	9·81±0·69	7·34±0·52	8·97±0·63	8·71	28·36	2·859
SepB	—	11·14±0·79	10·26±0·74	9·65±0·68	10·35	14·40	1·429
SepIx	—	11·94±0·86	11·42±0·82	11·86±0·84	11·74	4·43	0·438
SdL	9·33±0·47	7·94±0·56	7·14±0·50	6·34±0·45	7·69	38·88	4·595
SdB	7·88±0·39	6·52±0·46	5·97±0·42	7·24±0·51	6·90	27·68	3·332
SdIx	8·70±0·43	7·42±0·52	6·83±0·48	6·90±0·49	7·46	25·07	2·902
AL	9·37±0·94	8·83±0·62	7·78±0·55	8·00±0·56	8·50	18·69	1·460
ATL	21·91±2·30	18·59±1·36	15·56±1·33	18·08±1·31	18·54	34·25	2·478
FlG	35·13±2·38	30·79±2·35	34·45±2·71	28·66±2·17	32·26	20·06	2·009
LfS	19·17±1·20	17·47±1·26	16·57±1·20	18·24±1·32	17·86	14·56	1·532
LfH	29·11±1·91	23·83±1·76	22·94±1·71	26·45±1·98	25·58	24·12	2·406
ScS	15·20±0·94	13·16±0·94	12·84±0·92	13·70±0·99	13·73	17·19	1·795
ScH	13·65±0·84	11·52±0·82	14·51±1·05	13·23±0·95	13·23	22·60	2·245
LfS : H	24·12±1·54	25·79±1·92	22·57±1·67	22·65±1·67	23·78	13·54	1·265
ScS : H	15·31±0·95	14·42±1·03	14·86±1·07	14·43±1·04	14·76	6·03	0·635
HbG	25·30±1·63	25·22±1·87	21·54±1·59	22·25±1·64	23·83	15·78	1·651
BrL : SepL	—	9·79±0·69	10·53±0·76	12·51±0·89	10·94	24·86	2·415
ScL : SpL	—	16·96±1·23	12·45±0·95	16·11±1·17	15·17	29·73	2·902
ScL : LfL	—	13·36±0·96	13·05±0·94	10·67±0·76	12·36	21·76	2·197

In Table IX the mean values for the leaf characters, together with the differences between them expressed as a percentage of the 2-year mean, are given for PMN 21 in the seasons 1931 and 1935. It will be observed that the percentages range from 0·1 to 19·6. It has already been shown (Table V (C)) that PMN 21 and PMN 44 are similar; this being so the seasonal behaviour of the one should run parallel to that of the other. When, therefore, the mean values of PMN 21 are adjusted on the basis of the seasonal behaviour of PMN 44, the percentage differences should be reduced if the actual values reflect environmental influences. The corrected values do indeed show reductions, as may be seen in the lower half of Table IX. We may take as an

TABLE IX. *Seasonal fluctuations in leaf characters (PMN 21; 1931 and 1935)*

The actual mean values are shown, and also values corrected for seasonal effect on the basis of a control population.

Actual values	LfS	LfH	LfS : H	LfL	LfB	LfTh
M' (1931)	13·98	4·27	3·42	27·21	6·02	1·08
M'' (1935)	14·83	4·73	3·34	27·25	7·33	0·95
M (of both)	14·41	4·50	3·38	27·23	6·68	1·02
$\frac{M'-M''}{M} \times 100$	5·901	10·222	2·367	0·147	19·626	12·808
Corrected values						
M' (1931)	14·53	4·59	3·31	27·25	6·81	0·91
M'' (1935)	14·50	4·65	3·35	27·78	6·86	0·94
M (of both)	14·52	4·62	3·33	27·52	6·84	0·93
$\frac{M'-M''}{M} \times 100$	0·207	1·299	1·201	1·926	0·732	3·226

example the figures for leaf spread. The appropriate mean values for this measurement were:

	1931	1935	4-year mean
PMN 44 ...	14·51	15·42	15·08
PMN 21 ...	13·98	14·83	

Now if the PMN 21 values are multiplied by the factor 4-year mean ÷ yearly mean for PMN 44, we have $13{\cdot}98 \times 1{\cdot}0393 = 14{\cdot}53$, and $14{\cdot}83 \times 0{\cdot}9779 = 14{\cdot}50$. The percentage difference is thus reduced from 5·9 to 0·2.

Influence of age on population data

It was not found possible to obtain reliable estimates of the characters of the reproductive parts during the first year of growth on account of the failure of some plants to produce scapes until the second year; moreover, the first season leaf characters were not a guide to the second-year performance. The second-year leaf lengths have invariably been found to exceed the value for the previous season. Leaf breadth, however, proved to be a more erratic character, the first season's measurements sometimes exceeding those of the second season as is shown in Table X. The greater breadth of leaf in the first year was found to occur most commonly in populations producing comparatively few leaves at that stage. When measuring maximum size characters, the date of sampling was a matter of importance. It will be noted from Table X that by 8 July the leaf length of population PMN 54 had almost attained its maximum. In some populations, however, the end of July was the date of maximum leaf development.

TABLE X

Differences between one- and two-year-old populations

	Mean values				Coefficient of variation			
	Leaf length		Leaf breadth		Leaf length		Leaf breadth	
Population	1st year	2nd year	1st year	2nd year	1st year	2nd year	1st year	2nd year
PMN 21	24·20±·540	27·21±·530	7·75±·239	6·02±·154	22·52±1·65	18·79±1·36	30·90±2·36	25·83±1·92
PMN 44	24·21±·407	27·28±·418	7·87±·201	6·06±·136	19·59±1·23	19·36±1·22	29·62±1·95	25·90±1·68

Effect of date of sampling on leaf length and leaf breadth values (PMN 54)

	Mean values			Coefficient of variation		
Character	5 May	8 July	16 August	5 May	8 July	16 August
LfL	16·14±·496	29·91±·646	30·67±·643	30·93±2·37	21·80±1·60	21·13±1·54
LfB	7·36±·247	29·91	11·31±·291	33·52±2·61		26·01±1·94

Habitat sampling

The reliability of the method of habitat sampling adopted was tested by examining collections from the same habitats made in different years. Two habitats, A and B, were sampled in the years 1928 and 1930 respectively, and in 1933 the same habitats were revisited and other two samples obtained. In 1934 these four samples were sown and transplanted into the garden, each in a randomized arrangement of six rows of seventeen plants. The populations were examined in 1935. The significance of the data, in the form of the ratio D/E_d, is presented in Table XI. It will be seen that when the characters of the duplicate samples A' and A'' were compared, and similarly those of B' and B'', the mean differences were less than three times their errors. The samples may therefore be regarded as truly representative of their habitats. When, however, the collections from the two different habitats A and B were compared, the mean differ-

TABLE XI. *Reliability of habitat sampling*

Inter- and intra-habitat collection comparisons.

	$\frac{\text{Difference}}{\text{Error of } D}$ of mean values			$\frac{\text{Difference}}{\text{Error of } D}$ of C values		
Character	Habitat $A'-A''$	Habitat $A-B$	Habitat $B'-B''$	Habitat $A'-A''$	Habitat $A-B$	Habitat $B'-B''$
LfL	1·05	16·44	1·87	1·26	0·49	0·34
LfB	0·51	12·13	0·22	0·70	0·83	0·19
LfTh	1·64	11·07	1·27	0·27	0·15	1·24
ScL	1·10	12·55	0·35	0·33	1·43	1·02
ScTh	1·35	22·84	1·02	0·10	0·21	0·66
SpL	0·32	8·81	1·28	1·25	0·01	0·31
SpD	2·44	1·07	0·05	1·45	0·57	1·68
BrL	0·10	3·38	1·55	0·88	0·31	1·04
BrB	0·86	10·90	0·31	0·47	1·34	2·88
BrIx	0·57	4·98	1·34	0·32	0·80	0·56
SepL	0·50	2·33	0·70	0·28	0·57	0·29
SepB	0·20	15·23	0·78	1·67	2·18	0·31
SepIx	0·32	11·13	0·11	0·51	1·63	0·48
SdL	0·01	18·49	0·05	0·02	0·03	0·01
SdB	0·04	8·85	0·05	0·02	0·01	0·07
SdIx	0·03	9·66	0·08	0·06	0·00	0·04
AL	0·14	1·71	0·11	0·67	1·92	0·00
ATL	0·69	1·62	0·81	0·65	0·25	0·87
FlG	0·18	17·71	0·40	0·49	0·62	0·25
LfS	1·27	8·32	0·75	0·96	0·27	2·44
LfH	0·18	2·12	1·22	0·42	0·07	0·98
ScS	0·00	4·62	0·06	1·08	0·80	0·70
ScH	1·15	15·45	0·68	0·48	1·62	1·04
LfS : H	0·97	0·23	1·58	0·45	0·92	0·73
ScS : H	1·84	18·43	0·00	0·66	0·18	1·01
HbG	0·73	9·35	0·73	1·96	3·16	0·32
BrL : SepL	0·06	2·35	2·16	0·75	1·04	0·00
ScL : SpL	0·89	0·67	1·51	0·67	0·80	0·41
ScL : LfL	2·27	1·87	0·76	1·55	0·39	1·71

ences, especially for the size and habit of growth characters, were clearly significant, as can be seen from column 3 of the table. The significances of the differences between the coefficients of variation are given in the last three columns. The only difference which was greater than three times its error was that between habitats *A* and *B* for the character habit grade, the erect population from habitat *B* having the lower value.

Where seed was difficult to obtain owing to the effect on seed production of high winds, grazing animals, etc., random samples of 200 or more plants were taken and seeded in isolation at Edinburgh. As already explained PMN 44 was a sample obtained in this way from plants taken from the natural habitat of PMN 21 in order to test the validity of the method. The similarity between these two populations, as shown in Table V (C), proves that no significant discrepancy arises through adopting this method of sampling.

Cultural methods

It has already been shown that a population reacts significantly to seasonal differences and to differences of locality. In any one season, soil irregularities or gradients and cultural treatment will tend to invalidate the results unless precautions are taken to minimize their effects. In this connexion the arrangement of sample plots and the choice of the number of plants to represent a population are matters of importance.

In order to establish the most suitable plot arrangement, a trial area was planted with 408 plants of population PMN 44 in twelve rows of thirty-four plants. This allowed for arbitrary divisions into smaller plots of varying size and shape, ranging from halves, lengthwise or crosswise, to single cross rows of only twelve plants. The plant characters examined for the purposes of the test were those which reflected growth vigour, e.g. leaf and scape length. Each of the 408 plants received an identification number and was examined separately.

(*a*) *Variability within plots*. The coefficients of variation for leaf and scape length for some of the plot arrangements are given in Table XII. It will be seen that, although the values for the 204-plant plots approach more closely the values for the whole plot than do those of the 102-plant plots, yet when the lengthwise, 3×34, arrangement of the latter is examined, the greatest deviations from the whole plot value are found to be only 1·14 and 1·55 per cent for leaf length in the first and second year respectively, and 1·05 per cent for scape

TABLE XII. *Variability within and between plots*

Character	Number of plants, and plot shape		No. of plots	Variability within plots: 1st year *C* values: Range	1st year *C* values: Difference	2nd year *C* values: Range	2nd year *C* values: Difference	Variability between plots: Greatest % difference between means: 1st year	2nd year
Leaf length	408	12 × 34	1	24·06	—	20·16	—	—	—
	204	6 × 34	2	24·10–23·92	0·18	20·31–19·44	0·87	3·2	6·4
	204	12 × 17	2	24·41–23·05	1·36	20·36–19·72	0·64	6·3	4·8
	102	3 × 34	4	25·13–22·92	2·21	20·33–18·61	1·72	6·9	9·0
	102	6 × 17	4	27·01–20·00	7·01	22·19–17·81	4·38	11·9	11·3
	51	3 × 17	8	26·78–16·65	10·13	23·38–15·04	8·34	23·1	14·3
Scape length	408	12 × 34	1			12·51	—		—
	204	6 × 34	2			13·21–11·67	1·54		2·3
	204	12 × 17	2			12·66–12·37	0·29		1·4
	102	3 × 34	4			13·56–11·50	2·06		4·1
	102	6 × 17	4			14·18–10·81	3·37		3·7
	51	3 × 17	8			14·78–10·70	4·08		5·2

length. This arrangement of 102 plants may therefore be considered as a *representative sample* affording a reasonably accurate estimate of the variability of the whole population.

(*b*) *Variability between plots.* The mean values for the various plot arrangements were found to follow the trend of the coefficients of variation inasmuch as the differences between the extreme means increased as the number of plants in the sample decreased. These differences, expressed as percentages of their general mean values, are given for a few arrangements in Table XII. It was also observed, especially in the case of first-year plants, that, in arrangements of the same number of plants, differences were generally greater for short than for long plots, owing to the presence of a strip of lower soil fertility traversing the area in a more or less diagonal direction. Although the adoption of a lengthwise arrangement of plots reduced the effect of the fertility gradient, its influence was not entirely eliminated. For example, the scape length mean values for the four lengthwise 102-plant plots (3 × 34), given in order of plot position, exhibit the following trend: Plot I, 43·50 cm. ± 0·549; II, 42·18 ± 0·566; III, 41·76 ± 0·476; and IV, 42·00 ± 0·494. The significances of these values as represented by the ratios D/E_d were: comparing Plots I and II, 1·673; I and III, 2·395; I and IV, 2·029; II and III, 0·568; II and IV, 0·239; and III and IV, 0·350.

If, instead of treating the total of 408 plants as a single population, there are assumed to be four populations of 102 plants scattered as strips of seventeen plants at random in six blocks, the soil effect can be still further reduced. For example, the widest ratio D/E_d for scape length in the case of comparisons between the four lengthwise 102-plant plots was, as previously stated, 2·395, but between the four randomized populations the equivalent ratio was reduced to 1·096. It may therefore be concluded that 102 plants constitute a reliable sample of the larger population and that, although for observing the general characteristics of collections lengthwise plots (three rows of thirty-four plants) are preferable to other arrangements, greater accuracy is obtainable by adopting a randomized plot arrangement.

IV. DISCUSSION

Continuous variation is the least desirable form of diversity for use in classification. Among the larger units it may be troublesome only to a limited extent, but when small "subspecific" units are dealt with it is a problem that must constantly be faced. It is natural first to attempt to place such striking variations as may exist into

categories, but this resolves itself into a recording of the existence of either a limited number of conspicuous types, or an infinite number of phenotypes which may take their form from such unsubstantial causes as the temporary combination of characters in individual plants and the diverse modifications of local environment. The random cataloguing of phenotypes, moreover, tends to mask the real significance of character combinations, since a unit based on some character peculiarity will have the same *taxonomic* value wherever it happens to occur, whereas *biologically* its importance may depend on its proportional representation in different parts of its range. The ecotype concept postulates that the innumerable character combinations become sorted out and grouped by the environment in virtue of the constitution of the plant as a whole, and not because of any phenotypic character in particular. The concept, therefore, may elucidate a taxonomic problem which has not been fully solved by the prevailing methods. Quantitative and continuous characters assume greater importance than qualitative and discontinuous in the differentiation of races of "subspecific" rank. Moreover, cognizance has to be taken of the different combinations and proportions in which the same characters may appear locally under the selective influence of the prevailing environment. The problem, therefore, becomes one of assessing average character values and the significance of the differences between ecologically distributed populations, rather than one of describing individual variations.

In the sea plantains, discontinuous variations are few and have little importance. In this connexion the sporadic occurrence, in widely separated regions, of golden chlorophyll-deficient types may be mentioned, and also the presence, in varying numbers and colour intensities, of anthocyanin spots on the leaves of some individual plants in almost every population. Nevertheless, discontinuity in both these instances has reference only to the presence or absence of the characters. There are, however, many quantitative characters which vary continuously within populations. The ranges of these in different populations nearly always overlap, and even if they do not a series could be arranged so that there could be continuous variation throughout.

The experimental garden method may be regarded as an attempt to compare various hereditary constitutions by reducing them to a common environmental denominator. It is unnecessary to say that the environment chosen must be reasonably suited to all the material. For example, sea plantains from Greenland could not be tested at

Edinburgh because they failed to develop scapes under normal daylight, although they readily ripened seed when the period of daylight was lengthened artificially. In order to study the hereditary differences between races, it is important that errors, due to (1) ununiformity of environment and (2) methods of sampling, should either be avoided, or assessed to determine how far they may affect the results. Although absolute uniformity of environment is an unattainable ideal, yet it is possible to minimize the errors due to environmental influences by careful cultivation and planning. In the experimental garden the chief difficulties that are likely to be encountered are gradients or irregularities in soil fertility and the effects of shading or exposure. Planning might consist of some application of the yield trial technique that has been devised by statisticians for agricultural research. One difficulty, however, is that though the experimentalist may be able to cope with the individual records of one representative sample, say 100 plants, of each of the populations he wishes to compare, yet it may be impracticable for him to replicate such samples. A small uniformity trial (Table XII) shows that if the representative samples be sown side by side in single plots, as is convenient for observation, allowance must be made for a certain amount of error due to soil fertility. This error could be considerably reduced, however, if small portions of the samples were arranged at random in a series of blocks. While the comparison of duplicated samples of a population in the same season and place may show that their differences of means and variabilities are seldom significant (Table V (A and B)), similar comparisons in different localities (Table VI) or different seasons (Table VII) may indicate the magnitude of error that should be expected if dissimilarities of environment are disregarded.

Comparison of populations is completely dependent upon efficient methods of sampling the characters, but at the same time the labour of recording makes it desirable to reduce the observations upon each plant to a minimum. Quantitative characters have wide ranges of magnitude within the plant itself (Tables I and II) so that random sampling of the various parts of a plant would involve very large errors. It might be true that such errors would tend to cancel out in the estimation of population mean, but it is also requisite that a record should at least indicate the relation of an individual plant to others in respect of a character. Some form of selective sampling is therefore necessary, and in this connexion Pearson's (1901) methods of obtaining "homotypes" and of testing their validity can be

adapted to the present type of investigation (Table III). Finally it is necessary to determine the minimum number of plants that will afford a sample representative of the population, and this may be deduced from the data of a uniformity trial (Table XII).

Even when these various difficulties have been taken into account it is possible, in the plantains, to compare distinct habitat populations with some satisfaction, for differences may not only be significant, but may frequently be of magnitudes far transcending the unavoidable errors of cultivation or sampling (Table V). Thus it may be assumed that variations of a true hereditary nature are indeed present.

V. Summary

1. The classification of evolutionary units on the basis of experimental facts is termed Experimental Taxonomy; it is suggested that while experimental and orthodox taxonomy are not antagonistic, any immediate attempt to absorb the experimental results into the existing system would be undesirable and would only lead to confusion.

2. The present paper is an introduction to the experimental study of *Plantago maritima* L. and closely allied species, and describes the methods adopted in studying the quantitative characters and variability of habitat populations under the comparatively uniform conditions of an experimental garden. The investigations comprise the sampling of habitats, the arrangement of habitat samples in the garden, the choice of characters, the sampling of individual plants, the examination of "errors" due to non-hereditary causes, and the formulation of methods of assessing the character values of populations.

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EXPERIMENTAL TAXONOMY

II. INITIAL POPULATION DIFFERENTIATION IN *PLANTAGO MARITIMA* L. OF BRITAIN

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(With 4 figures in the text)

CONTENTS

I. Introduction

It is customary to regard the species unit as the convenient starting point for evolutionary discussion. Doubtless this practice has been favoured because the species, notwithstanding its numerous interpretations, does on the whole approximate more nearly to an evolutionary entity than do the less well-defined units of lower rank. The *species* and the *variety*, however, differ only in degree, and there is actually no valid reason why the latter should not also be employed for the elucidation of evolutionary problems. On the basis of the accepted criteria it may sometimes be difficult to decide whether certain observable differences really warrant taxonomic recognition, and it is often a matter of personal preference whether species or varietal rank is awarded to a group. But there is no definite reason why demonstrable natural grouping should inevitably be relegated to the units of traditional taxonomy a new terminology resulting from a new orientation of the biological facts might be more appropriate. For instance it might be demonstrated by field and garden

experiment that the initiation of population differentiation is more important biologically than the magnitude of the resulting morphological differences: in this case the unit could be based on the causal factors, factors perhaps external to the plants themselves. The degree of morphological distinctness would under these circumstances have only a diagnostic value and no taxonomic status. Dependable criteria for the classification of initial population differentiation are undoubtedly difficult to obtain in the herbarium, and in consequence Hall (1929) proposed that small units should be described only in a numbered or lettered list of minor variations, and that they should be left in this provisional category until their status could be determined by experiment or other exact methods. Hall's suggestion has much to recommend it because in this way the known facts would be made available to the experimentalist without the systematist having to "commit himself when evidence is lacking" and "without introducing false concepts as to relationships".

In the first paper of this series (Gregor *et al.* 1936) it was advocated that a separate taxonomic system should be developed for recording the results of the experimental analysis of wild populations, because it was felt that any immediate attempt to absorb the experimental results into the existing system would be undesirable and could only lead to confusion. The present paper gives the results of an attempt to determine the biological significance of the initial character groupings which differentiate wild populations, and to illustrate a possible way of expressing taxonomically the findings of experimentation.

To establish the arrangement of characters in Nature, however, it is first necessary to obtain *representative* samples from the wild, and second to minimize the effect of fluctuating variability. Reliable samples of local populations are generally more easily obtainable than samples representative of a whole species. For this reason subspecific assemblages are to be preferred for the study of initial differentiation within an intrafertile group. The sea plantains of Britain (*Plantago maritima* L.) afford excellent material not only because the members of the population are interfertile, but because while the distribution round the coastline of the mainland is continuous, that of the adjacent islands and of the inland mountains is discontinuous. In an introductory paper (Gregor, 1930) it was shown that population differentiation could occur in the absence of spatial isolation, but at that time little information was available regarding the number and variability of characters affected by ecological separation. Information was then also lacking concerning the relative

effects of ecological and geographical isolation on the magnitude of population differences. Thirty-two population samples collected from habitats in Britain have now been grown in the experimental garden at Edinburgh and 100 or more plants of each have been studied by the methods previously described (Gregor *et al.* 1936). In addition a number of smaller samples were examined, but the data relating to these have not been included in the accompanying tables.

The distribution of Plantago maritima *in Britain*

The distribution of *Pl. maritima* in Britain is general throughout the coastal regions, but inland it occurs only in localized stations. In this it is remarkably similar to *Armeria vulgaris* Willd. which is one of the few other species in which these conditions obtain. For a better understanding of how this distribution has come about, it is of interest to note the present occurrence of these two species in Iceland. There, while they again occur generally on the coast, they are also common inland, although they are absent from the nunataks explored by Steindór Steindórsson. It is therefore likely that in Britain *Plantago maritima* spread post-glacially from the coastal districts to the higher mountains of Scotland and England subsequently being displaced from the intermediate regions. The occasional establishment in suitable habitats of migrants from the coastal regions may still take place, but it seems more probable that the mountains are the loci from which most present-day inland migrations radiate.

In the British mountain habitats *Pl. maritima* grows on thinly populated rock ledges, and at lower elevations it is most commonly found among boulders and escarpments in the vicinity of streams, some of these habitats being of very recent origin. No records are available as to the permanency of the lowland populations, but in all probability they are displaced by more aggressive species as the habitats become stabilized. Shade, rather than altitude, seems to be the limiting factor to lowland establishment, as is evident from the fact that at low elevations in regions of tall vegetation *Pl. maritima* is found only on the margins of streams and paths. Actually seed production is more abundant in the lowland habitats than in the subalpine (3000 ft.) zone where the plants are more or less scattered.

Since streams leading from mountain habitats provide the most probable lines of dispersal, plantain populations found on the banks of streams having a common mountain source have been

regarded, for the purposes of this investigation, as having a similar locus of dispersion; only habitats which are topographically unconnected have been considered as truly isolated. The inland population of the sea plantains of Britain has been regarded by White (1869) as representing three species: *Pl. maritima* L., *Pl. alpina* L. and *Pl. serpentina* Vill., but there seems to be no justification for making such distinctions, and the whole population should be considered as belonging to a single species, *Pl. maritima* L.

In contrast to the restricted inland distribution the coastal distribution is continuous. *Pl. maritima* has been recorded from every one of Watson's (1883) vice counties which possesses a coastline. In this paper coastal populations from the Western Isles are not treated with the coastal populations of the mainland on account of their geographically isolated position. In Fig. 1 the inland habitats from which samples were taken are indicated by black circles, hatched circles mark the position of the coastal populations sampled, while black triangles denote other inland records. The following samples have been critically studied in the experimental garden:

A. *Inland.*

I. Ben Lui locus (Perthshire):

PMN 17, collected 23. x. 27 at 500 ft., from the eroded shore of Loch Dochart. (Examined 1931.)

PMN 18, coll. 5. ix. 28 at 800 ft., from gravelly alluvium near Coninish. (1930.)

PMN 28, coll. 5. ix. 28 at 2000 ft., from banks of a stream. (1930.)

II. Ben Cruachan locus (Argyllshire):

PMN 16, coll. 23. x. 27 at 100 ft., from the banks of the river Awe. (1929.)

PMN 38, coll. 12. ix. 29 at 700 ft., from a *Festuca* pasture. (1933.)

PMN 39, coll. 11. ix. 29 at 120 ft., from rocky shore of Loch Awe. (1933.)

III. Unconnected habitats:

PMN 21, coll. 29. ix. 28 near Blair Atholl (Perthshire) at 450 ft., from gravelly alluvium adjacent to the river Garry. (1931.)

PMN 40, coll. 9. ix. 29 in Glen Shiel (Ross-shire) at 70 ft., from the banks of the River Shiel. (1934.)

PMN 55, coll. 10. ix. 30 on Carrick Hill (Ayrshire) at 750 ft., from areas adjacent to road. (1933.)

PMN 90, coll. 12. ix. 33 near Gillerthwaite, Ennerdale (Cumberland), at 500 ft., from a rocky hillside. (1936.)

B. *Island.*

I. Lewis (Hebrides):

PMN 47, coll. 6. ix. 30 near Stornoway from coastal waterlogged mud. (1932.)

PMN 48, coll. 7. ix. 30 near Stornoway from partially populated sea cliff. (1932.)

PMN 49, coll. 8. ix. 30 near Valtos from a meadow above highest tide mark. (1932.)

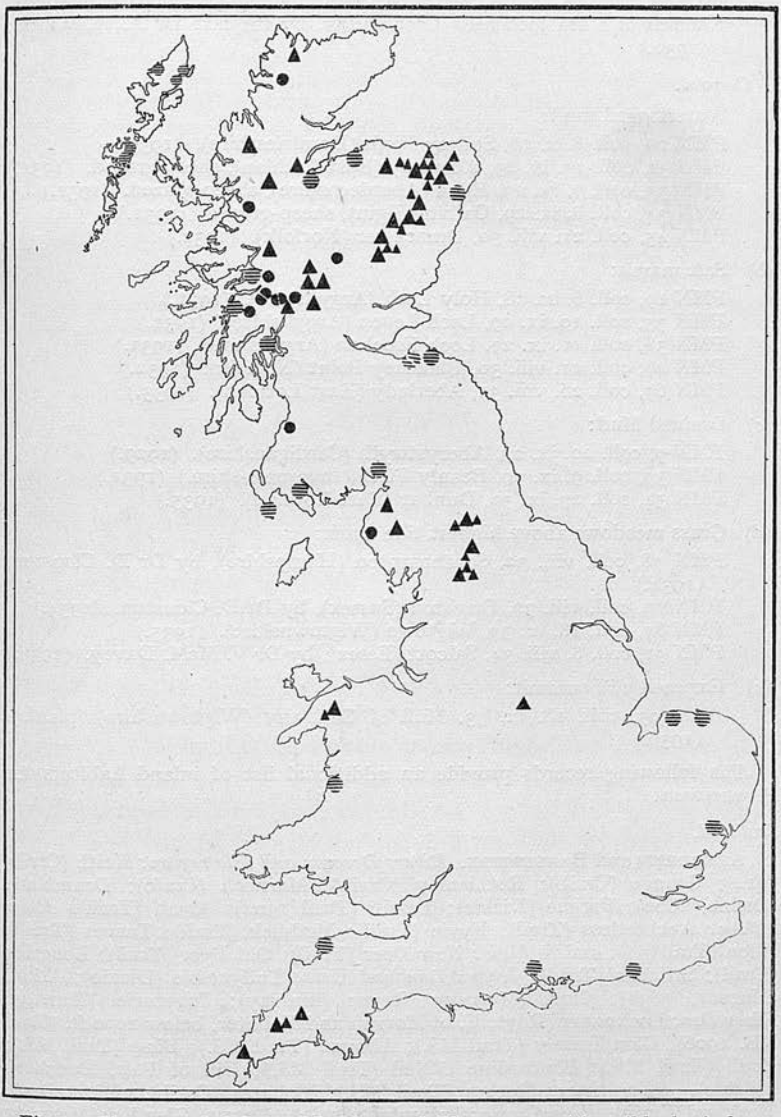

Fig. 1. The recorded Inland habitats of *Plantago maritima* (black circles and triangles), and the Coastal habitats sampled (hatched circles).

II. North Uist (Hebrides):

PMN 23, coll. 10. ix. 28 from a cattle-grazed pasture on the shores of a sea loch near Lochmaddy by the late Dr A. R. Wilson. (1930.)

PMN 25, coll. 12. ix. 28 from a cattle- and sheep-grazed pasture on the shores of a sea loch near Lochmaddy, by the late Dr A. R. Wilson. (1930.)

C. *Coastal.*

(*a*) Waterlogged mud:

PMN 20, coll. 8. x. 28, Solway Firth (Dumfriesshire). (1930.)
PMN 32, coll. 17. ix. 29, Aberlady (East Lothian), sheep-grazed. (1931.)
PMN 33, coll. 7. ix. 29, Ellon (Aberdeenshire), sheep-grazed. (1931.)
PMN 34, coll. 8. ix. 29, Culbin (Elgin), sheep-grazed. (1931.)
PMN 45, coll. 21. viii. 30, Brancaster (Norfolk). (1932.)

(*b*) Salt marsh:

PMN 19, coll. 8. ix. 28, Holy Loch (Argyllshire). (1931.)
PMN 35, coll. 10. ix. 29, Loch Leven (Argyllshire). (1931.)
PMN 36, coll. 11. ix. 29, Loch Feochan (Argyllshire). (1931.)
PMN 46, coll. 21. viii. 30, Blakeney Point (Norfolk). (1932.)
PMN 67, coll. 26. viii. 31, Aberlady (East Lothian). (1933.)

(*c*) Drained Mud:

PMN 9, coll. 20. ix. 27, Aberystwyth (Cardiganshire). (1929.)
PMN 37, coll. 9. ix. 29, Beauly Firth (Inverness-shire.) (1931.)
PMN 54, coll. 27. ix. 30, Dunbar (East Lothian). (1935.)

(*d*) Grass meadows above highest tide mark:

PMN 78, coll. viii. 32, Southampton (Hampshire), by Dr D. Clouston. (1934.)
PMN 80, coll. viii. 32, Brighton (Sussex), by Dr D. Clouston. (1934.)
PMN 87, coll. 18. ix. 33, Wigtown (Wigtownshire). (1935.)
PMN 91, coll. 8. viii. 34, Salcott (Essex), by Dr V. McM. Davey. (1936.)

(*e*) Exposed cliff summit:

PMN 93, coll. 18. ix. 33, Mull of Galloway (Wigtownshire) (plants). (1936.)

The following records provide an additional list of inland habitats for *P. maritima*:

Scotland.

ABERDEEN and BANFFSHIRE. *Rivers Deveron and Isla region:* Keith (Craib, 1912); Grange (Craib); Rothiemay (Craib); Marnoch (Craib); Drumblade (Dickie, 1860); Forgue (Dickie); Turriff (Trail 1902); Alvah (Trail). *River Ythan:* Auchterless (Trail); Fyvie (Trail); Methlick (Trail); Tarves (Trail); Ellon (Trail); *N. and S. Ugie:* New Deer (Trail); Old Deer (Trail); Longside (Trail); Strichen (Trail). *Rivers Don and Urie:* Tullynessle (Dickie); Alford (Murray, 1836); Clatt (Murray); Rayne (Murray); Inverurie (Murray). *River Dee:* Lochnagar (Roy); E. of Morven and Ballater, below 2000 ft. (Trail MS. 1906); Glen Tanner (Trail MS.); Aboyne (Trail MS.); Birse (Trail MS.); Coull (Trail MS.); Kincardine O'Neil (Trail MS.); Hill of Fair, Banchory (Dickie). *River Spey:* Rothes (Trail MS.); Boharm (Craib). *River Desk:* Deskford (Craib). *River Boyne:* Ordiquhill (Craib). ANGUS. Glen Esk (Murray); Glen Clova, 1853, Balfour (Anonymous, 1902); Glen Isla, 1837, Balfour, Herb. Bot. Gard. Edinb.; Airlie (Gardiner, 1848). DUMBARTONSHIRE. Ben Vorlich, 1866, Balfour, Herb. Bot. Gard. Edinb. INVERNESS-SHIRE. Ben Nevis, 1876, Sadler, Herb. Bot. Gard. Edinb. PERTHSHIRE. Loch Rannoch, 1881, Evans, Herb. Bot. Gard. Edinb.; Meall Ghaordie, 1870, Balfour (Anonymous, 1902);

Cam Craig, Loch Earn, 1837, Balfour, Herb. Bot. Gard. Edinb.; Breadalbane, 2600 ft. (White, 1898). Ross-shire. Achilty, 1868, White, Herb. Bot. Gard. Edinb.; Slioch (Druce, 1929); Benula, Cannich, Adam. Sutherlandshire. Ben Hope, 2600 ft. (Melvill, 1889).

England.

Cornwall. St Day (Davey, 1902); Bodmin (Davey); St Neot (Davey); Launceston (Davey). Cumberland. Moota Hill, between Aspatria and Cockermouth (Hodgson, 1898); Head of Fusedale (Baker, 1885). Yorkshire. Cronkleyfell, 1790 ft. (Baker, 1863); High Force, 1730 ft. (Baker, 1863); Winch Bridge, 1836, Herb. Bot. Gard. Edinb.; Askrigg, between there and Carperby, Good (written communication); Seamerdale (Baker, 1863); Arncliffe, between there and Kilnsey (Bains, 1840); Grassington, between there and Kilnsey (Miall, 1862); Settle (Lees, 1888). Derbyshire. Alfreton, 1804, Backhouse, Herb. Bot. Gard. Edinb.

Wales.

Carnarvonshire. Snowdon, 2600 ft. (Williams, 1912, p. 360). Crags of Glyder Faur, 1865. Backhouse, Herb. Bot. Gard. Edinb.

II. The examination of characters

Mean values

The methods of sampling habitat populations, of growing the samples in the experimental garden and of assessing their character values have already been dealt with in the paper previously mentioned (Gregor *et al.* 1936). The samples, according to their source, have been grouped in Table I into the three primary habitat categories—Inland, Island and Coastal; the samples from the Coastal areas are further subdivided into five ecologically distinctive habitat groups thus: (*a*) waterlogged mud, (*b*) typical salt marsh, (*c*) drained mud, (*d*) grassland above highest tide mark, and (*e*) exposed cliff summit. The individual sample mean values and their standard errors, calculated from 100 or more observations, are presented for each character studied and, in addition, a general mean is given for the Inland and Island populations and for each subdivision of the Coastal samples. The characters have been previously defined elsewhere (Gregor *et al.* 1936, p. 329) with the exception of scape volume, which is an approximate value in litres for plant size, calculated from the formula $\pi\left(\frac{scape\ spread}{2}\right)^2 \times$ scape height.

From a perusal of the mean figures for the Coastal categories (*a*), (*b*), (*c*) and (*d*) it will be noticed that for the characters scape spread, scape height, scape length, scape thickness, spike length, scape volume, leaf length, leaf breadth, leaf spread, leaf height and seed length there is a progressive increase in size from habitat (*a*) to habitat (*d*), while for the character spike density there is a progressive decrease in density in the same direction. The differences between the values for

TABLE I. *Mean values*

Habitats	Samples PMN	Habit grade	Scape spread/ height	Scape spread in.	Scape height in.	Scape length cm.	Scape thickness mm.	Spike length cm.	Scape volume litres
Inland: I	17	2·00 ± 0·102	1·56 ± 0·030	18·3 ± 0·37	11·9 ± 0·28	30·2 ± 0·61	1·55 ± 0·030	6·91 ± 0·163	3·45 ± 0·177
	18	2·75 ± 0·042	1·26 ± 0·016	17·8 ± 0·22	14·3 ± 0·17	36·3 ± 0·37	1·82 ± 0·015	9·74 ± 0·120	3·85 ± 0·131
II	16	1·76 ± 0·076	1·54 ± 0·022	18·4 ± 0·24	12·1 ± 0·20	32·0 ± 0·44	1·41 ± 0·017	6·85 ± 0·129	3·37 ± 0·122
	38	2·26 ± 0·084	1·43 ± 0·026	16·0 ± 0·32	11·5 ± 0·30	31·1 ± 0·69	1·44 ± 0·024	7·89 ± 0·206	2·58 ± 0·169
	39	2·32 ± 0·097	1·62 ± 0·039	18·8 ± 0·37	12·1 ± 0·30	33·7 ± 0·62	1·35 ± 0·017	7·47 ± 0·169	3·69 ± 0·219
III	40	2·42 ± 0·074	1·45 ± 0·023	19·9 ± 0·33	14·0 ± 0·21	36·3 ± 0·45	1·66 ± 0·023	9·35 ± 0·172	4·55 ± 0·186
	55	2·63 ± 0·081	1·37 ± 0·027	18·0 ± 0·28	13·4 ± 0·24	35·6 ± 0·49	1·46 ± 0·021	8·85 ± 0·169	3·52 ± 0·159
	21	2·81 ± 0·065	1·22 ± 0·018	18·7 ± 0·25	15·6 ± 0·23	39·3 ± 0·51	1·87 ± 0·022	9·72 ± 0·168	4·47 ± 0·158
	90	2·85 ± 0·063	1·10 ± 0·018	16·2 ± 0·28	14·8 ± 0·21	38·9 ± 0·52	1·84 ± 0·019	10·17 ± 0·194	3·21 ± 0·146
Mean		2·42	1·39	18·01	13·30	34·82	1·60	8·55	3·63
Island: I	47	1·21 ± 0·056	2·27 ± 0·092	8·5 ± 0·22	4·1 ± 0·14	14·9 ± 0·40	1·30 ± 0·025	3·82 ± 0·148	0·29 ± 0·021
	48	1·66 ± 0·080	2·01 ± 0·078	13·5 ± 0·39	7·5 ± 0·30	23·8 ± 0·65	1·40 ± 0·026	6·56 ± 0·226	1·34 ± 0·111
	49	2·71 ± 0·074	1·15 ± 0·021	14·4 ± 0·26	12·7 ± 0·21	33·8 ± 0·45	1·83 ± 0·025	10·15 ± 0·178	2·20 ± 0·098
II	25	1·89 ± 0·066	1·89 ± 0·069	16·0 ± 0·26	9·1 ± 0·21	26·7 ± 0·40	1·59 ± 0·021	6·94 ± 0·148	1·95 ± 0·091
	23	1·91 ± 0·049	1·58 ± 0·024	16·2 ± 0·25	10·6 ± 0·20	28·7 ± 0·44	1·68 ± 0·020	8·17 ± 0·135	2·39 ± 0·111
Mean		1·88	1·78	13·72	8·80	25·58	1·56	7·13	1·63
Coastal: (*a*)	32	1·29 ± 0·054	1·98 ± 0·055	13·1 ± 0·31	7·1 ± 0·23	22·1 ± 0·54	1·72 ± 0·029	6·62 ± 0·181	1·10 ± 0·069
	33	1·56 ± 0·072	1·68 ± 0·038	14·5 ± 0·31	8·9 ± 0·23	27·1 ± 0·52	1·96 ± 0·027	8·00 ± 0·162	1·64 ± 0·096
	34	1·69 ± 0·083	1·57 ± 0·039	12·1 ± 0·36	7·9 ± 0·23	22·7 ± 0·54	1·76 ± 0·036	6·46 ± 0·195	1·14 ± 0·094
	20	1·80 ± 0·064	1·55 ± 0·029	16·7 ± 0·20	11·4 ± 0·21	32·3 ± 0·46	2·07 ± 0·019	10·11 ± 0·166	2·68 ± 0·102
	45	1·97 ± 0·083	1·41 ± 0·033	16·0 ± 0·42	11·7 ± 0·32	35·7 ± 0·75	1·81 ± 0·033	11·44 ± 0·290	2·76 ± 0·189
Mean		1·66	1·64	14·48	9·40	27·98	1·864	8·53	1·86
(*b*)	19	2·00 ± 0·095	1·46 ± 0·039	15·4 ± 0·29	11·1 ± 0·33	31·8 ± 0·66	2·11 ± 0·029	9·25 ± 0·202	2·34 ± 0·136
	35	2·09 ± 0·076	1·51 ± 0·033	15·0 ± 0·36	10·2 ± 0·24	27·8 ± 0·48	1·74 ± 0·030	7·19 ± 0·175	2·02 ± 0·133
	46	2·22 ± 0·066	1·37 ± 0·019	17·7 ± 0·40	13·0 ± 0·28	36·5 ± 0·63	1·83 ± 0·026	10·62 ± 0·242	3·64 ± 0·218
	36	2·25 ± 0·063	1·42 ± 0·029	15·1 ± 0·32	11·1 ± 0·22	31·4 ± 0·58	1·78 ± 0·020	9·01 ± 0·150	2·23 ± 0·127
	67	2·59 ± 0·071	1·31 ± 0·024	18·4 ± 0·34	14·3 ± 0·28	38·7 ± 0·58	2·03 ± 0·027	10·75 ± 0·210	4·01 ± 0·219
Mean		2·23	1·41	16·32	11·94	33·24	1·898	9·36	2·85
(*c*)	9	2·87 ± 0·064	1·00 ± 0·017	17·6 ± 0·30	17·8 ± 0·23	44·5 ± 0·51	2·23 ± 0·027	9·82 ± 0·149	4·64 ± 0·195
	37	2·97 ± 0·057	0·90 ± 0·017	15·6 ± 0·38	17·4 ± 0·30	45·3 ± 0·63	2·25 ± 0·028	11·44 ± 0·265	3·67 ± 0·209
	54	3·33 ± 0·056	0·81 ± 0·013	16·5 ± 0·29	20·3 ± 0·22	49·3 ± 0·52	2·70 ± 0·030	12·60 ± 0·217	4·53 ± 0·204
Mean		3·06	0·903	16·57	18·50	46·37	2·39	11·29	4·28
(*d*)	91	2·78 ± 0·075	1·08 ± 0·018	18·7 ± 0·30	17·7 ± 0·29	45·4 ± 0·66	2·11 ± 0·025	10·43 ± 0·199	5·14 ± 0·203
	80	2·99 ± 0·033	1·13 ± 0·017	23·3 ± 0·39	20·9 ± 0·30	52·5 ± 0·67	2·51 ± 0·038	13·96 ± 0·278	9·42 ± 0·342
	78	3·05 ± —	1·10 ± 0·015	24·8 ± 0·46	22·4 ± 0·42	53·8 ± 1·10	2·33 ± 0·043	13·60 ± 0·375	11·18 ± 0·570
	87	3·23 ± 0·061	0·84 ± 0·015	17·5 ± 0·32	21·1 ± 0·24	50·6 ± 0·54	2·64 ± 0·026	12·64 ± 0·199	5·32 ± 0·217
Mean		3·01	1·04	21·08	20·53	50·58	2·40	12·66	7·77
(*e*)	93	1·41 ± 0·059	2·33 ± 0·058	14·3 ± 0·24	6·4 ± 0·16	19·4 ± 0·35	1·22 ± 0·017	4·13 ± 0·093	1·10 ± 0·059

Habitats	Samples PMN	Leaf length cm.	Leaf breadth mm.	Leaf thickness mm.	Leaf spread in.	Leaf height in.	Leaf spread/ height	Spike density	Bract length mm.
Inland: I	17	23·1 ± 0·49	5·70 ± 0·201	1·04 ± 0·016	9·1 ± 0·31	3·12 ± 0·115	2·98 ± 0·086	—	—
	18	27·7 ± 0·38	6·88 ± 0·125	1·06 ± 0·012	9·4 ± 0·16	3·69 ± 0·081	2·80 ± 0·042	—	—
II	16	22·7 ± 0·37	4·97 ± 0·144	1·00 ± 0·013	9·2 ± 0·21	3·00 ± 0·085	3·20 ± 0·078	—	—
	38	19·7 ± 0·59	4·97 ± 0·181	0·82 ± 0·015	11·0 ± 0·30	2·58 ± 0·078	4·47 ± 0·116	13·4 ± 0·20	2·48 ± 0·036
	39	21·4 ± 0·57	4·87 ± 0·155	0·83 ± 0·012	10·7 ± 0·30	2·75 ± 0·090	4·12 ± 0·115	13·1 ± 0·21	2·27 ± 0·031
III	40	25·1 ± 0·43	6·60 ± 0·188	0·80 ± 0·012	12·0 ± 0·26	4·38 ± 0·130	2·86 ± 0·064	14·4 ± 0·21	2·78 ± 0·033
	55	21·1 ± 0·39	5·38 ± 0·136	0·82 ± 0·011	11·2 ± 0·20	3·28 ± 0·081	3·55 ± 0·072	15·0 ± 0·21	—
	21	27·3 ± 0·37	7·33 ± 0·159	0·95 ± 0·012	14·8 ± 0·24	4·73 ± 0·134	3·34 ± 0·087	13·8 ± 0·24	2·80 ± 0·039
	90	21·8 ± 0·33	5·80 ± 0·162	0·79 ± 0·010	11·6 ± 0·22	3·74 ± 0·093	3·20 ± 0·059	14·1 ± 0·19	2·65 ± 0·032
Mean		23·32	5·83	0·901	11·00	3·47	3·39	13·97	2·60
Island: I	47	11·5 ± 0·41	3·87 ± 0·134	0·98 ± 0·014	3·48 ± 0·142	1·04 ± —	3·36 ± 0·135	12·6 ± 0·23	2·29 ± 0·043
	48	18·2 ± 0·50	4·94 ± 0·183	0·90 ± 0·013	6·18 ± 0·238	1·70 ± —	3·85 ± 0·118	14·1 ± 0·27	2·58 ± 0·061
	49	22·2 ± 0·45	6·77 ± 0·182	0·98 ± 0·012	7·71 ± 0·249	2·46 ± 0·099	3·39 ± 0·110	14·9 ± 0·27	2·93 ± 0·050
II	25	20·4 ± 0·45	5·35 ± 0·155	1·18 ± 0·015	8·99 ± 0·227	2·80 ± 0·093	3·51 ± 0·105	—	—
	23	23·2 ± 0·42	4·68 ± 0·122	1·10 ± 0·013	9·23 ± 0·216	2·82 ± 0·079	3·57 ± 0·075	—	—
Mean		19·10	5·12	1·03	7·12	2·16	3·54	13·87	2·60
Coastal: (*a*)	32	15·8 ± 0·52	4·14 ± 0·181	1·02 ± 0·018	6·1 ± 0·22	1·81 ± 0·073	3·51 ± 0·098	13·9 ± 0·21	2·48 ± 0·030
	33	20·1 ± 0·53	5·90 ± 0·175	1·24 ± 0·034	7·0 ± 0·25	2·02 ± 0·063	3·03 ± 0·129	12·9 ± 0·18	2·74 ± 0·032
	34	16·6 ± 0·56	3·89 ± 0·168	1·18 ± 0·018	6·6 ± 0·26	1·71 ± 0·077	4·09 ± 0·141	—	—
	20	22·1 ± 0·35	5·45 ± 0·118	1·18 ± 0·012	9·7 ± 0·18	2·75 ± 0·059	3·81 ± 0·065	—	—
	45	21·0 ± 0·55	6·40 ± 0·232	0·97 ± 0·017	8·4 ± 0·36	2·24 ± 0·102	3·93 ± 0·119	12·0 ± 0·19	2·69 ± 0·050
Mean		19·12	5·16	1·12	7·56	2·11	3·67	12·93	2·64
(*b*)	19	23·3 ± 0·59	5·44 ± 0·199	1·25 ± 0·018	9·1 ± 0·30	2·26 ± 0·088	4·30 ± 0·157	12·0 ± 0·14	2·55 ± 0·034
	35	24·0 ± 0·58	6·47 ± 0·242	1·19 ± 0·020	8·3 ± 0·26	2·20 ± 0·094	4·13 ± 0·141	—	—
	46	23·3 ± 0·54	7·41 ± 0·213	1·08 ± 0·016	10·3 ± 0·36	2·75 ± 0·123	4·06 ± 0·116	11·6 ± 0·26	2·79 ± 0·067
	36	22·1 ± 0·44	5·64 ± 0·145	1·14 ± 0·015	7·7 ± 0·21	2·07 ± 0·069	4·03 ± 0·109	12·7 ± 0·14	2·33 ± 0·032
	67	24·8 ± 0·48	7·18 ± 0·186	0·98 ± 0·017	12·1 ± 0·31	2·93 ± 0·088	4·32 ± 0·106	13·3 ± 0·19	2·40 ± 0·031
Mean		23·50	6·43	1·13	9·50	2·44	4·17	12·40	2·52
(*c*)	9	26·9 ± 0·37	9·38 ± 0·161	1·20 ± 0·020	14·4 ± 0·28	4·57 ± 0·165	3·52 ± 0·101	—	—
	37	34·5 ± 0·56	9·16 ± 0·210	1·33 ± 0·018	13·0 ± 0·29	4·11 ± 0·136	3·37 ± 0·089	11·1 ± 0·15	2·87 ± 0·039
	54	36·1 ± 0·47	12·20 ± 0·247	1·17 ± 0·012	18·4 ± 0·24	5·24 ± 0·136	3·68 ± 0·078	13·4 ± 0·22	3·15 ± 0·036
Mean		32·50	10·25	1·23	15·27	4·64	3·52	12·25	3·01
(*d*)	91	30·9 ± 0·54	9·65 ± 0·156	1·04 ± 0·017	15·7 ± 0·28	5·52 ± 0·155	2·97 ± 0·068	11·6 ± 0·13	2·82 ± 0·028
	80	35·5 ± 0·64	11·48 ± 0·270	1·06 ± 0·014	18·9 ± 0·43	6·63 ± 0·243	3·13 ± 0·086	12·0 ± 0·18	3·30 ± 0·046
	78	32·2 ± 0·63	11·74 ± 0·412	1·00 ± 0·016	19·5 ± 0·45	7·08 ± 0·248	2·82 ± 0·069	12·3 ± 0·25	2·97 ± 0·063
	87	32·9 ± 0·48	11·53 ± 0·225	1·07 ± 0·011	15·1 ± 0·28	4·84 ± 0·130	3·27 ± 0·066	13·0 ± 0·17	2·83 ± 0·033
Mean		32·88	11·10	1·04	17·30	6·02	3·05	12·23	2·98
(*e*)	93	14·9 ± 0·29	5·80 ± 0·162	0·77 ± 0·011	7·21 ± 0·19	2·90 ± 0·069	2·48 ± 0·033	15·1 ± 0·20	1·99 ± 0·024

Table I (continued)

Habitats	Samples PMN	Bract breadth mm.	Bract index	Sepal length mm.	Sepal breadth mm.	Sepal index	Seed length mm.	Seed breadth mm.	Seed index
Inland: I	17	—	—	—	—	—	—	—	—
	18	—	—	—	—	—	—	—	—
II	16	—	—	—	—	—	—	—	—
	38	1·15 ± 0·013	2·17 ± 0·026	2·43 ± 0·023	1·04 ± 0·010	2·34 ± 0·027	2·40 ± 0·015	0·99 ± 0·006	2·42 ± 0·015
	39	1·11 ± 0·012	2·06 ± 0·026	2·37 ± 0·020	1·02 ± 0·011	2·33 ± 0·027	2·35 ± 0·015	1·03 ± 0·007	2·28 ± 0·016
III	40	1·32 ± 0·015	2·14 ± 0·023	2·51 ± 0·020	1·12 ± 0·009	2·25 ± 0·021	2·38 ± 0·018	1·02 ± 0·007	2·35 ± 0·016
	55	—	—	—	—	—	2·30 ± 0·015	0·99 ± 0·006	2·33 ± 0·015
	21	1·24 ± 0·013	2·25 ± 0·030	2·47 ± 0·019	1·11 ± 0·013	2·25 ± 0·025	2·43 ± 0·018	1·01 ± 0·008	2·43 ± 0·016
	90	1·21 ± 0·011	2·19 ± 0·022	2·35 ± 0·014	1·07 ± 0·008	2·21 ± 0·018	2·40 ± 0·011	0·99 ± 0·006	2·43 ± 0·016
Mean		1·21	2·16	2·43	1·07	2·28	2·38	1·01	2·37
Island: I	47	1·37 ± 0·020	1·68 ± 0·030	2·46 ± 0·026	—	—	2·57 ± 0·016	1·05 ± 0·007	2·46 ± 0·016
	48	1·24 ± 0·024	2·08 ± 0·039	2·49 ± 0·049	—	—	2·13 ± 0·019	0·94 ± 0·006	2·27 ± 0·020
	49	1·37 ± 0·021	2·14 ± 0·032	2·78 ± 0·030	—	—	2·37 ± 0·012	1·02 ± 0·005	2·33 ± 0·014
II	25	—	—	—	—	—	—	—	—
	23	—	—	—	—	—	—	—	—
Mean		1·33	1·97	2·58	—	—	2·36	1·00	2·35
Coastal: (*a*)	32	1·33 ± 0·012	1·87 ± 0·023	—	—	—	2·37 ± 0·017	0·99 ± 0·006	2·41 ± 0·014
	33	1·55 ± 0·013	1·78 ± 0·015	—	—	—	2·62 ± 0·015	1·05 ± 0·005	2·51 ± 0·013
	34	—	—	—	—	—	2·53 ± 0·015	1·06 ± 0·006	2·39 ± 0·013
	20	—	—	—	—	—	—	—	—
	45	1·32 ± 0·016	2·02 ± 0·026	2·62 ± 0·027	—	—	—	—	—
Mean		1·40	1·89	2·62	—	—	2·51	1·03	2·44
(*b*)	19	1·41 ± 0·015	1·83 ± 0·018	—	—	—	2·59 ± 0·018	1·05 ± 0·007	2·47 ± 0·014
	35	—	—	—	—	—	2·68 ± 0·016	1·10 ± 0·007	2·44 ± 0·015
	46	1·40 ± 0·025	2·00 ± 0·030	2·72 ± 0·032	—	—	2·75 ± 0·018	1·00 ± 0·006	2·76 ± 0·017
	36	1·44 ± 0·014	1·62 ± 0·017	—	—	—	2·73 ± 0·017	1·07 ± 0·007	2·56 ± 0·015
	67	1·32 ± 0·014	1·83 ± 0·019	2·45 ± 0·012	1·18 ± 0·012	2·10 ± 0·022	2·84 ± 0·017	1·10 ± 0·007	2·59 ± 0·018
Mean		1·39	1·82	2·59	1·18	2·10	2·72	1·06	2·56
(*c*)	9	—	—	—	—	—	—	—	—
	37	1·69 ± 0·019	1·70 ± 0·020	—	—	—	2·82 ± 0·017	1·13 ± 0·007	2·51 ± 0·014
	54	1·48 ± 0·011	2·14 ± 0·022	2·61 ± 0·018	1·34 ± 0·010	1·95 ± 0·018	2·97 ± 0·023	1·11 ± 0·008	2·69 ± 0·018
Mean		1·59	1·92	2·61	1·34	1·95	2·90	1·12	2·60
(*d*)	91	1·37 ± 0·013	2·07 ± 0·019	2·57 ± 0·020	1·32 ± 0·012	1·96 ± 0·020	2·96 ± 0·015	1·10 ± 0·007	2·71 ± 0·016
	80	1·56 ± 0·016	2·11 ± 0·022	2·81 ± 0·026	1·35 ± 0·010	2·08 ± 0·019	2·98 ± 0·028	1·08 ± 0·008	2·79 ± 0·023
	78	1·52 ± 0·026	1·97 ± 0·025	2·56 ± 0·035	1·25 ± 0·019	2·05 ± 0·030	3·01 ± 0·028	1·07 ± 0·010	2·78 ± 0·020
	87	1·38 ± 0·012	2·07 ± 0·022	2·47 ± 0·015	1·28 ± 0·010	1·94 ± 0·016	3·01 ± 0·022	1·10 ± 0·008	2·73 ± 0·015
Mean		1·46	2·06	2·60	1·30	2·01	2·99	1·09	2·75
(*e*)	93	1·19 ± 0·013	1·69 ± 0·021	2·17 ± 0·020	1·09 ± 0·010	1·99 ± 0·019	2·03 ± 0·011	0·92 ± 0·006	2·22 ± 0·016

Habitats	Samples PMN	Anther length mm.	Anther tip length mm.	Bract length/ sepal length	Scape length/ spike length	Scape length/ leaf length	Flowering grade
Inland: I	17	—	—	—	4·44 ± 0·086	1·33 ± 0·031	—
	18	—	—	—	3·78 ± 0·064	1·35 ± 0·027	—
II	16	—	—	—	4·78 ± 0·079	1·42 ± 0·025	—
	38	1·89 ± 0·019	0·284 ± 0·006	1·02 ± 0·010	4·03 ± 0·064	1·65 ± 0·027	7·18 ± 0·165
	39	1·80 ± 0·018	0·271 ± 0·006	0·96 ± 0·011	4·60 ± 0·074	1·62 ± 0·028	7·45 ± 0·177
III	40	2·06 ± 0·014	0·299 ± 0·006	1·11 ± 0·011	3·97 ± 0·063	1·47 ± 0·022	5·02 ± 0·136
	55	—	—	—	4·12 ± 0·066	1·72 ± 0·024	4·13 ± 0·158
	21	2·10 ± 0·021	0·282 ± 0·005	1·15 ± 0·013	4·13 ± 0·063	1·46 ± 0·018	3·77 ± 0·123
	90	1·98 ± 0·018	0·335 ± 0·006	1·14 ± 0·012	3·91 ± 0·057	1·82 ± 0·029	2·94 ± 0·124
Mean		1·97	0·294	1·08	4·20	1·54	5·08
Island: I	47	2·01 ± 0·026	0·249 ± 0·007	0·93 ± 0·016	4·15 ± 0·107	1·39 ± 0·040	6·85 ± 0·231
	48	2·04 ± 0·032	0·250 ± 0·006	1·04 ± 0·016	3·82 ± 0·099	1·43 ± 0·030	3·97 ± 0·107
	49	2·23 ± 0·029	0·243 ± 0·008	1·05 ± 0·016	3·30 ± 0·047	1·56 ± 0·024	3·30 ± 0·089
	25	—	—	—	3·93 ± 0·067	1·35 ± 0·029	—
II	23	—	—	—	3·59 ± 0·061	1·27 ± 0·023	—
Mean		2·09	0·247	1·01	3·76	1·40	4·71
Coastal: (*a*)	32	2·19 ± 0·033	0·242 ± 0·009	—	3·39 ± 0·051	1·50 ± 0·032	2·43 ± 0·146
	33	2·36 ± 0·024	0·269 ± 0·009	—	3·42 ± 0·050	1·48 ± 0·027	1·96 ± 0·106
	34	2·16 ± 0·031	0·267 ± 0·009	—	3·63 ± 0·067	1·44 ± 0·030	3·28 ± 0·175
	20	—	—	—	3·31 ± 0·050	1·48 ± 0·029	—
	45	2·36 ± 0·027	0·270 ± 0·008	1·04 ± 0·016	3·20 ± 0·053	1·73 ± 0·025	2·88 ± 0·126
Mean		2·27	0·262	1·04	3·39	1·53	2·64
(*b*)	19	2·19 ± 0·038	0·243 ± 0·010	—	3·51 ± 0·067	1·53 ± 0·023	2·09 ± 0·114
	35	2·04 ± 0·027	0·291 ± 0·007	—	3·91 ± 0·067	1·18 ± 0·023	5·52 ± 0·187
	46	2·32 ± 0·027	0·270 ± 0·008	1·03 ± 0·018	3·46 ± 0·050	1·61 ± 0·032	6·60 ± 0·189
	36	2·11 ± 0·028	0·255 ± 0·009	—	3·43 ± 0·039	1·44 ± 0·020	3·32 ± 0·101
	67	2·02 ± 0·019	0·285 ± 0·006	0·97 ± 0·010	3·67 ± 0·059	1·59 ± 0·025	4·17 ± 0·204
Mean		2·14	0·269	1·00	3·60	1·47	4·34
(*c*)	9	—	—	—	4·60 ± 0·083	1·66 ± 0·022	—
	37	2·58 ± 0·030	0·279 ± 0·008	—	3·84 ± 0·078	1·34 ± 0·018	1·91 ± 0·098
	54	2·18 ± 0·018	0·300 ± 0·006	1·22 ± 0·012	3·95 ± 0·057	1·38 ± 0·015	1·23 ± —
Mean		2·38	0·290	1·22	4·13	1·46	1·57
(*d*)	91	2·27 ± 0·017	0·252 ± 0·006	1·10 ± 0·009	4·44 ± 0·066	1·51 ± 0·025	7·64 ± 0·102
	80	2·32 ± 0·020	0·279 ± 0·007	1·18 ± 0·013	3·83 ± 0·069	1·50 ± 0·018	6·75 ± 0·161
	78	2·31 ± 0·022	0·248 ± 0·007	1·17 ± 0·019	4·04 ± 0·104	1·70 ± 0·028	7·02 ± 0·260
	87	2·22 ± 0·014	0·287 ± 0·005	1·15 ± 0·011	4·08 ± 0·060	1·55 ± 0·017	1·01 ± —
Mean		2·28	0·267	1·15	4·10	1·57	5·61
(*e*)	93	2·00 ± 0·017	0·234 ± 0·006	0·92 ± 0·010	4·81 ± 0·079	1·33 ± 0·021	7·89 ± 0·153

the characters scape thickness, spike length, leaf height, and spike density however, do not reach the 0·05 level of significance (Fisher, 1932, Table of *t*) and therefore these characters cannot be said to exhibit any significant effect of habitat conditions. If the habitat category (*d*) be disregarded, then in addition to the above the characters habit grade, leaf thickness, anther tip length and the ratio scape length : spike length show mean values increasing towards habitat (*c*), while the values for scape spread : height and scape length : leaf length become progressively less, i.e. the samples tend to become more erect and the leaves to be longer in proportion to the scapes under conditions prevailing in (*c*) habitats. The differences between the means for the characters leaf thickness, anther tip length and the ratio scape length : leaf length are, however, not significant. The characters leaf spread : height, bract length, bract breadth, bract index and anther length fail to follow a sequence.

Now if the characters which exhibit no significant sequence or lack sequence altogether are disregarded then the following remain: habit grade, scape spread : height, scape spread, scape height, scape length, scape volume, leaf length, leaf breadth, leaf spread, seed length and scape length : spike length. With the exception of the character scape length : spike length, a ratio indicating that the spikes become shorter in proportion to the scape as the scapes increase in length, all these characters represent measurements either of growth habit or size of scapes, seeds and leaves. These data, therefore, lead to the conclusion that while the dimensions of floral parts, e.g. seeds, may be influenced to some extent by general plant size, and therefore indirectly by habitat conditions, it is primarily the habit and size of the scapes, and the leaf dimensions which are affected by the environment. It would indeed be difficult to establish a geographical sequence within the sampled area in the distribution of such character owing to this marked influence of the habitat factors. For example the differences in growth-habit and size between the samples PMN 32 and 67 from distinctive but adjacent habitats in East Lothian are considerably greater than those occurring between the samples PMN 36 and 46 collected from ecologically similar habitats as far apart as Argyllshire and Norfolk respectively.

The fractionation of plantain populations into localized habitat races by environment is repeated in Lewis, one of the Western Islands. Only three samples have been examined from this island but they are representative of different types of habitat; PMN 47 belongs to the (*a*) habitat category, PMN 48 was collected from a

partially populated cliff habitat, while PMN 49 was collected from a coastal meadow in many respects equivalent to the (*d*) category of the mainland. If habit grade and scape length, leaf length and scape volume are again taken as the respective criteria of habit of growth and size, it will be seen from Table I that there is, as previously, a significant progressive increase in the erectness and size of the sample constituents from the waterlogged to the meadow habitat. In this instance, however, the size increase is also noticeable in the lengths of both bracts and sepals, although the difference between PMN 47 and 48 for the latter character is not significant.

It is plain from the above examples that dwarf growth accompanies a high water table; but high winds and the influence of the grazing animal produce similar effects. For example, PMN 93, from an exposed cliff habitat subject to sheep grazing, resembled in many respects samples PMN 47, 32, 33 and 34 collected from waterlogged mud flats. In the natural habitats the parallelism was even more pronounced than in the experimental garden because in the wild the leaves of all these populations were short (1–4 cm. in length) and more or less cylindrical. In culture, however, PMN 93 exhibited a more cushion-like appearance than did the mud-flat samples, largely owing to the crowding together of the numerous short leaves and scapes. Of all the population samples examined from Britain PMN 93 had the highest value for the ratio scape spread : height, $2{\cdot}33 \pm 0{\cdot}058$, the next highest in the series being the Island population PMN 47 with $2{\cdot}27 \pm 0{\cdot}092$; the difference, however, is not significant. In PMN 93 the size characters scape length, leaf length and scape volume have mean values which fall between the values for PMN 47 and 32 both of which samples are characterized by the small size of their component plants. Decumbent growth-habit and dwarfness are therefore not peculiar to water-logged habitats.

In the Inland samples, as far as the growth-habit and the size of the vegetative organs are concerned, the mean values fall within the Coastal range. A few of the mean values for the floral characters (bract breadth, bract index, sepal breadth, sepal index, seed length and seed index), however, fall beyond the Coastal range, but only in the case of bract index (PMN 21), sepal breadth (PMN 39) and sepal index (PMN 38, 39, 40, 55, 21) are these deviations significant. Of the Inland characters sepal index alone has mean values which do not overlap those of the Coastal series. Unfortunately the data for this character are lacking for several populations, but in so far as the figures are available the Inland samples are, on the average, shown

to possess sepals narrower in proportion to their length than do the Coastal samples.

It might have been expected that as the altitude of the Inland habitats increased, the size of the population components would decrease, but it has not been possible to establish any regular sequence in this direction. For example PMN 17, collected from a waterlogged habitat at an elevation of 500 ft. is seen to have size characters considerably smaller than those of PMN 18 from a habitat at 800 ft. However PMN 28, a numerically small sample from a habitat at an altitude 1200 ft. higher than the habitat of PMN 18 and 1500 ft. higher than the habitat of PMN 17, but still on the same stream, was found to be appreciably smaller than PMN 17. Under these circumstances therefore, the tendency for a vertical diminution of size characters is largely masked by the diversity of the habitat conditions at similar altitudinal levels.

In determining the relative times of flowering of the samples a scale of flowering stages was employed, and each plant in a sample was classed as belonging to one of eleven grades, the earliness increasing from grade I to grade II. If, in order to eliminate possible seasonal effects, the values for the year 1931 are compared by themselves it will be observed that some of the samples differ significantly from each other, e.g. the difference between the values for PMN 32 and 35 is thirteen times greater than its error. While no connexion between flowering time and latitude can be established, the averages of the mean values for the different habitat categories suggest that the samples from the (*a*) and (*c*) categories tend to be later flowering then those from (*b*) and (*d*). Even after the individual samples were adjusted on the basis of the seasonal behaviour of a control sample the same relative order was maintained, the adjusted average values for the habitat categories being: for (*a*), 2·74; (*b*) 4·09; (*c*) 1·68; and for (*d*) 5·88. However, in Lewis the sample PMN 47 from an (*a*) habitat flowered significantly earlier than PMN 49 from a (*d*) category, ($D/E_d = 14{\cdot}4$). From a consideration of these data it would seem that local environmental peculiarities play a considerable part in determining the flowering time of these populations.

Range values

While the mean values provide a satisfactory basis for assessing the differences between the genetically impure plantain assemblages, the sample ranges can be usefully employed in detecting the distribution of peculiar variates. It has already been mentioned that the

Inland mean values for the character sepal index do not overlap the corresponding values for the Coastal samples. When, however, the ranges for this character are examined (Table II) it will be seen that continuity in respect of the individual variates is established and that only the variates at the upper end of the range are peculiar to the Inland samples. The same is true for the character bract index.

The Island samples possess variates more dwarf than any found either in the Inland or Coastal samples, as may be seen from the leaf length, scape length, scape height and scape spread : height ranges. That plant size tends to be smaller in the Island samples can be substantiated by reference to the mean values of samples from equivalent habitats on the Mainland. For example the Mainland equivalent of PMN 47 is PMN 32 and of PMN 49 is PMN 80; their respective mean values for scape length are 14·9, 22·1, 33·8 and 52·5 cm., and for leaf length are 11·5, 15·8, 22·2 and 35·5 cm.

The salient feature of the summarized ranges of the Coastal habitat categories is the presence of a high degree of overlapping. Moreover, the extreme variates do not appear to group themselves in any particular geographical order, although for the (*c*) habitat category the largest variates have been found in a southern population and the smallest in a northern one. The sample mean values do not, however, confirm this sequence.

The characters leaf pubescence and leaf spot

Leaf pubescence. The leaves were examined under a 12× lens and the degree of hairiness of the sample components was classified into nine arbitrary grades thus: (1) glabrous, (2) very few scattered hairs on margins, (3) few scattered hairs on margins, (4) a considerable number of hairs on margins, (5) hairs on margins and very few scattered hairs on lower surfaces, (6) hairs on margins and scattered hairs on lower surface, (7) hairs on margins and scattered hairs on upper surface, (8) hairs on margins and scattered hairs on both surfaces, and (9) thinly pubescent.

The percentage number of plants occurring in each grade is summarized in Table III according to the habitats. If the grades of maximum pubescence for the margins, lower surfaces, and both surfaces, respectively grades (4), (6) and (9), are taken as the criteria of greatest pubescence, and the percentage number of variates occurring in these grades calculated, then the Island samples with 55% are the most hairy, the Inland with 34% are the next and the Coastal with 6% are the least pubescent. However, with the exception of

TABLE II. *Character ranges (summary)*

(For full character headings see Table I

Habitat	HbG	ScS:H	ScS in.	ScH in.	ScL cm.	ScTh mm.	SpL cm.	ScV cm.	LfL cm.	LfB mm.	LfTh mm.
Inland	1–5	0·8–3·2	9–29	5–22	18–53	1·0–2·5	4–16	0·6–13·2	12–46	2–13	0·5–1·7
Island	1–5	0·7–7·1	4–26	1–18	5–44	0·7–2·5	1–14	0·1– 8·0	3–39	2–13	0·6–1·5
Coastal:											
Total	1–5	0·5–5·6	4–31	2–27	7–69	0·8–3·5	1–21	0·1–20·4	4–51	1–22	0·5–2·0
Habitat (*a*)	1–4	0·8–3·8	4–24	2–20	7–51	1·0–2·9	2–21	0·1– 8·0	4–35	1–12	0·5–2·0
(*b*)	1–4	0·8–2·9	6–28	3–22	8–53	1·1–2·9	1–17	0·1–12·9	9–41	2–18	0·6–1·7
(*c*)	1–5	0·5–1·6	6–27	8–25	23–64	1·2–3·5	6–20	0·3–12·6	16–50	5–22	0·7–1·9
(*d*)	1–5	0·6–1·5	9–31	11–27	29–69	1·4–3·3	6–20	0·8–20·4	15–51	5–20	0·7–1·4
(*e*)	1–3	1·4–5·6	7–19	2–11	10–27	0·8–1·6	2– 6	0·1– 3·1	9–24	2–10	0·5–1·1

Habitat	LfS in.	LfH in.	LfS:H	SpD	BrL mm.	BrB mm.	BrIx	SepL mm.	SepB mm.
Inland	3–23	1·0–10	1·5–8·7	9–21	1·63–3·56	0·81–1·63	1·5–3·2	1·89–3·00	0·73–1·37
Island	2–15	1·0– 6	1·0–8·0	9–19	1·67–3·99	0·81–1·84	1·2–2·7	1·67–3·26	—
Coastal:									
Total	2–28	1·0–13	1·3–9·0	7–20	1·50–4·16	0·94–2·14	1·1–2·8	1·71–3·39	0·90–1·67
Habitat (*a*)	2–16	1·0– 8	1·6–8·0	8–20	1·71–3·86	0·99–1·93	1·4–2·7	2·19–3·00	—
(*b*)	2–22	1·0–10	1·3–9·0	8–18	1·63–4·16	0·99–1·93	1·1–2·6	1·93–3·39	0·94–1·50
(*c*)	5–23	1·0–11	1·5–8·5	7–18	2·06–4·07	1·24–2·14	1·1–2·8	2·14–3·00	1·03–1·63
(*d*)	8–28	2·5–13	1·8–6·4	9–19	1·97–4·11	1·16–1·71	1·3–2·7	2·06–3·34	0·99–1·67
(*e*)	3–12	1·5– 5	2·0–3·3	9–16	1·50–2·53	0·94–1·54	1·3–2·3	1·71–2·61	0·90–1·37

Habitat	SepIx	SdL mm.	SdB mm.	SdIx	AL mm.	ATL mm.	BrL/SepL	ScL/SpL	ScL/LfL
Inland	1·6–3·2	1·80–2·74	0·81–1·24	1·8–3·0	1·46–2·66	0·13–0·47	0·7–1·5	2·7–7·2	0·9–2·6
Island	—	1·63–3·26	0·81–1·29	1·8–3·1	1·46–2·83	0·09–0·39	0·7–1·4	2·5–8·5	0·7–2·6
Coastal:									
Total	1·5–2·7	1·76–3·59	0·77–1·46	1·8–3·5	1·63–3·09	0·09–0·47	0·7–1·5	1·8–7·4	0·7–2·8
Habitat (*a*)	—	1·89–3·17	0·77–1·33	1·8–3·1	1·76–2·87	0·13–0·43	0·9–1·4	1·8–5·5	0·8–2·8
(*b*)	1·5–2·6	1·97–3·51	0·77–1·37	1·9–3·5	1·63–2·91	0·09–0·47	0·8–1·4	2·4–6·3	0·7–2·8
(*c*)	1·6–2·7	2·27–3·51	0·90–1·46	1·8–3·1	1·76–3·09	0·17–0·47	1·0–1·5	2·2–6·6	0·9–2·2
(*d*)	1·6–2·6	2·40–3·59	0·90–1·37	2·2–3·3	1·84–2·74	0·13–0·43	0·9–1·5	2·7–6·5	1·0–2·2
(*e*)	1·6–2·5	1·76–2·36	0·77–1·07	1·8–2·7	1·63–2·40	0·13–0·39	0·7–1·2	3·5–7·4	0·9–2·0

grade (7), which has not been observed in Inland specimens, these three major habitat regions are represented by at least a few members of each grade. The percentages for the five habitat subdivisions of the Coastal samples do not reveal any tendency for the degree of hairiness to be influenced by the prevailing environmental conditions.

TABLE III. *Leaf pubescence (percentage plants occurring in each arbitrary grade)*

Grades ...	1	2	3	4	5	6	7	8	9	No. of plants
Inland (total)	1·3	21·4	14·0	8·1	24·1	24·3	0·0	4·2	2·6	1290
Island (total)	1·5	19·4	9·7	13·4	6·1	33·1	1·0	7·1	8·8	537
Coastal (total)	3·8	74·3	11·2	3·0	2·6	2·7	1·2	0·9	0·4	2203
Habitat (*a*)	5·0	82·0	5·5	1·0	2·5	1·7	0·2	1·5	0·5	596
(*b*)	4·6	72·5	10·7	4·4	1·5	2·2	0·7	2·2	1·1	542
(*c*)	2·4	77·1	14·6	1·9	2·7	0·8	0·2	0·3	0·0	625
(*d*)	1·8	68·9	14·5	4·7	3·6	4·1	0·3	0·9	1·2	338
(*e*)	6·9	38·2	15·7	6·9	17·6	4·9	1·0	6·9	2·0	102

Leaf spot. Spotting of the leaves due to the presence of anthocyanin pigment in some of the epidermal cells has been observed in 20% of the total number of plantains examined from habitats in Britain. The spots are usually small and of a deep wine-red colour, but their size, number per unit area and colour intensity vary greatly. The lack of spots is a recessive condition.

Spotted-leaved plants are much more frequent in some populations than in others, e.g. the percentage frequency of spotted plants in the Inland samples ranges from 0 to 45, in the Island from 6 to 53 and in the Coastal from 1 to 55. The average percentage occurrence for these three regions is, however, approximately the same being 17·9 for the Inland samples, 21·0 for the Island and 21·1 for the Coastal. As far as can be ascertained from the available data, the distribution of spotted plants is independent of latitudinal influence, percentages of 54 and 55 having been recorded from the North of Scotland and the South of England respectively. Nor can the conditions of the chosen habitat categories be said to control the distribution of spotted plants; for instances two apparently similar habitats have yielded samples of which one had 6% and the other 54%.

III. CHARACTER VARIABILITY

Habitat samples

For analytical purposes it is necessary to treat the individual characters as separate entities, although it is appreciated that the survival of a habitat population is dependent on the sum total of its

characters being at least tolerant of the prevailing environment. In comparing the variability of the different characters, different units of measurement have been used, e.g. mm., cm., inches, etc., therefore the variability has been expressed by the coefficient of variation (C). Table IV presents the average C values for each character for the major and minor habitat categories, and in addition the total average C value for each character. From an examination of the latter it will be seen that the variability is greatest for the leaves and scapes and least for the floral parts. That is, variability in relation to size is greatest for those characters which differentiate habitat populations. Moreover the C values for a given character tend to decrease as the size of the organs concerned increases, i.e. variability in relation to size is least in populations with large constituents. The reason for this may perhaps be more readily appreciated by reference to an example taken from the mean and range values for the character scape length (Tables I and II). In Table II the range for the (*a*) habitat category is given as 7–51 cm. and for the (*d*) category as 29–69 cm. The mean values for these two habitats are 28 and 46 cm. respectively, showing that for habitat (*a*) the mean of the samples was four times larger than the smallest variate, while for habitat (*d*) it was only one and a half times greater.

Although the coefficient of variation is a useful statistic for the comparison of the variability of a character in relation to size, yet it cannot be employed in assessing the actual variability of characters. When the size and habit of growth characters for the individual samples were examined it was found that their mean values were correlated with their C values, the coefficients of correlation being: scape length −0·80, scape height −0·84, spike length −0·64, leaf length −0·82, leaf breadth −0·76, and the ratio scape spread : height +0·73. These correlation values show that, as the means of the organs increase, and as the samples become more erect, the C values decrease. But for the characters spike length, leaf breadth and the ratio scape spread : height the mean values are also positively correlated with the standard deviations thus: spike length +0·66, leaf breadth +0·75, and scape spread : height +0·86. Therefore to arrive at the actual variability it is necessary to discount the effect of absolute size.

In making the comparison between the variability of Inland and Coastal samples it has been possible to eliminate the effect of differences in absolute size owing to the Inland mean values falling within the Coastal range. The average C values have been deter-

TABLE IV. *Coefficients of variation (summarized)*

Habitats	HbG	ScS/ScH	ScS	ScH	ScL	ScTh	SpL	ScV	LfL	LfB	LfTh	LfS	LfH	LfS/LfH	SpD
Inland (total)	33·2	17·4	16·9	18·7	15·6	13·5	20·1	47·1	19·6	28·9	14·4	23·2	29·5	23·8	15·1
Island (total)	36·9	30·0	21·6	27·1	20·0	15·6	26·0	59·6	25·0	31·6	13·4	32·6	35·6	31·3	13·1
Coastal (total)	32·8	20·2	20·4	21·2	17·2	14·0	21·4	54·5	21·3	28·6	15·5	27·5	34·9	27·4	13·6
Habitat (*a*)	44·3	24·5	23·3	27·9	22·1	16·1	25·0	64·5	28·3	36·5	18·5	35·9	41·3	31·6	14·1
(*b*)	34·9	20·9	21·7	23·7	18·4	14·4	21·6	61·1	23·1	31·9	15·8	31·5	39·2	31·3	13·3
(*c*)	21·0	18·3	20·8	14·6	12·8	12·8	19·6	50·9	15·3	21·3	14·7	19·5	30·2	27·4	14·9
(*d*)	18·8	14·2	15·5	13·4	12·6	11·8	17·7	36·6	15·3	20·4	12·3	18·0	27·9	21·0	12·9
(*e*)	42·5	25·3	17·3	25·6	18·2	14·4	22·7	54·3	19·4	28·1	14·6	26·4	24·0	13·5	13·2
Average C value	33·6	21·0	19·6	21·4	17·2	14·1	21·8	53·2	21·4	29·2	14·9	27·1	33·4	27·0	13·9

Habitats	BrL	BrB	BrIx	SepL	SepB	SepIx	SdL	SdB	SdIx	AL	ATL	BrL/SepL	ScL/SpL	ScL/LfL
Inland	13·2	10·6	11·3	7·9	9·7	10·3	6·4	6·7	6·6	9·3	20·0	10·8	15·9	16·5
Island (total)	14·1	11·7	12·1	9·7	—	—	8·5	7·9	8·9	9·9	20·2	11·2	19·8	20·8
Coastal (total)	13·0	10·0	10·5	7·9	8·7	9·3	7·9	7·8	7·3	8·5	21·8	10·3	16·2	15·8
Habitat (*a*)	12·9	9·0	11·2	7·3	—	—	8·9	8·2	7·8	9·1	23·6	11·1	15·8	18·8
(*b*)	14·3	11·1	10·4	8·2	9·9	10·5	8·5	8·3	8·1	9·7	21·4	11·1	16·0	17·4
(*c*)	12·5	9·4	11·1	7·0	7·5	9·1	8·1	8·3	7·4	8·1	20·6	9·8	17·6	12·6
(*d*)	12·1	9·9	9·4	7·7	8·6	9·0	6·7	7·0	5·9	6·9	20·5	9·7	15·6	12·3
(*e*)	12·4	10·8	12·4	9·3	9·0	9·4	5·6	6·7	7·1	8·5	23·8	10·7	16·6	15·9
Average C value	13·2	10·4	10·9	8·2	9·1	9·7	7·6	7·5	7·3	8·9	21·2	10·6	16·7	16·8

mined for the Inland samples and for an equivalent number of Coastal samples with an average mean value closely approximating to that of the Inland samples. For example, the average of the mean values for scape length for the nine Inland samples is 34·82 cm. (Table I), and for the particular nine Coastal samples taken it is

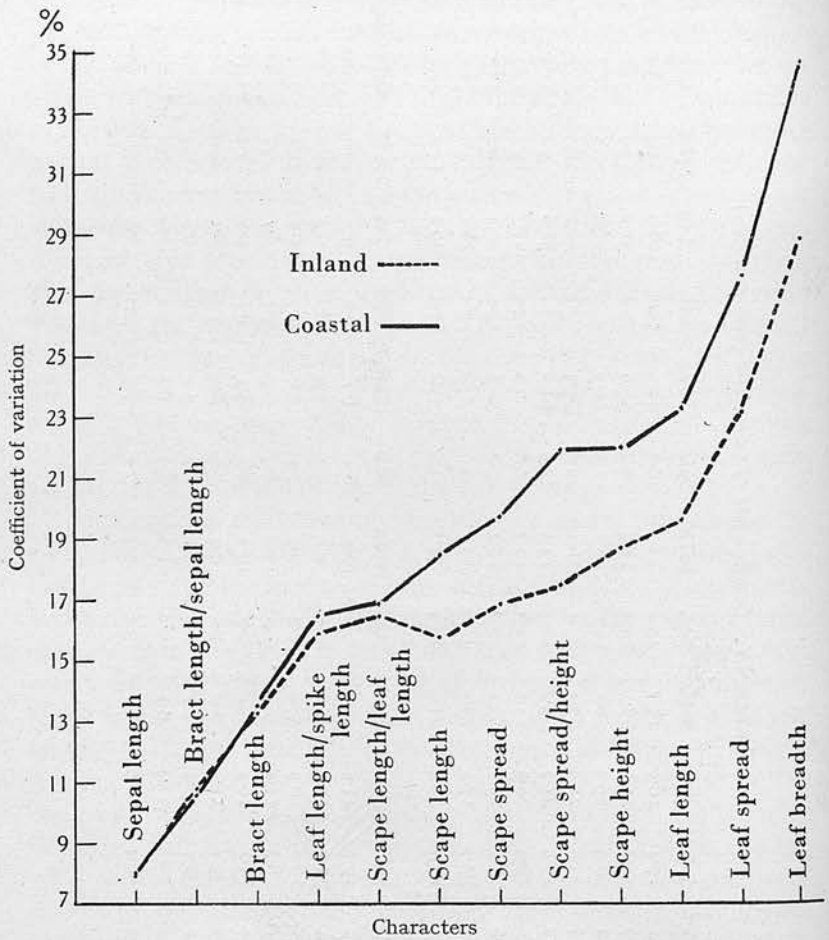

Fig. 2. The variability of Inland and Coastal populations compared.

34·99 cm.; the average C values for the Inland samples is 15·59% (Table IV) in comparison with 18·48% for the Coastal samples. In Fig. 2 the Inland and Coastal average C values, calculated in this manner, are given for the characters previously found to be influenced by habitat conditions, and also for the floral parts bract length and

sepal length. It is seen that when equivalent mean values are considered the Inland samples tend to have a lower variability than the Coastal.

When assessing the actual variability of the Coastal habitat categories, however, difficulty is experienced because equivalent size groups are not available.[1]

Wild growing populations

To obtain data with reference to the variability of populations when growing under natural conditions the habitats of samples PMN 32 (category (*a*)) and PMN 54 (category (*c*)) were again sampled. Individual plants were dug up and the leaf and scape characters were measured, the same procedure being observed as for the measurement of these characters under garden conditions. These samples are referred to as PMN 32 (2) and 54 (2). In Table V the coefficients of variation are given for the characters examined, together with the increase in size resulting from cultivation expressed as a percentage of the size of the equivalent wild sample. It will be seen from the latter that the increase under cultivation is greater in the case of PMN 32. Moreover, in comparison with PMN 32, PMN 32 (2) shows a significant decrease in variability relative to size in the characters scape length, leaf length and leaf breadth, a reduction which is not found in the case of PMN 54 (2).

TABLE V

	% increase in mean size under cultivation		Coefficient of variation			
			Habitat (*a*)		Habitat (*c*)	
Character	PMN 32 and 32 (2)	PMN 54 and 54 (2)	PMN 32	PMN 32 (2)	PMN 54	PMN 54 (2)
Scape length	403	68	24·6 ± 1·52	18·3* ± 1·33	10·3 ± 0·75	9·9 ± 0·69
Spike length	549	44	27·7 ± 2·09	23·7 ± 1·75	16·9 ± 1·25	18·7 ± 1·36
Leaf length	600	26	34·4 ± 2·38	25·2* ± 1·89	12·8 ± 0·93	11·5 ± 0·82
Leaf breadth	152	11	44·6 ± 3·70	20·7* ± 1·51	20·1 ± 1·49	21·1 ± 1·54
Average	426	37	32·8	22·0	15·0	15·3

* $D/E_d > 3$.

The evidence suggests that the modificatory influence of the wild environment can effect a considerable reduction of variability in relation to size and that this is most pronounced when dwarf growth is favoured by the environment.

[1] Since going to press B. Day and R. A. Fisher have published details of a method for the comparison of variability in populations having unequal means (*Annals of Eugenics*, 7, (4), 333–348, 1937).

IV. THE EFFECT OF AN ARTIFICIALLY IMPOSED ENVIRONMENT

The data furnished in Table I established the fact that racial differentiation had taken place in response to the prevailing environmental conditions in respect of the size and growth-habit characters. However, they do not supply evidence relative to the stage of development at which the plants were most sensitive to the selective influence of the environment. In order that the behaviour of parts of the same population growing under different conditions might be analysed experimentally a plantain sample, a mixture of three habitat collections, was sown in combination with herbage species in three series of eight plots as illustrated in Table VI. The series A and C were sown with, and B without, a nurse crop of oats.

TABLE VI. *Arrangement of plots and rate of seeding in lb. per acre*

Pl. maritima seeding rates	Series of plots A	B	C	Other species seeding rates
3	I	I	I	*Phleum pratense* 25
5	II	II	II	*Trifolium repens* 2
10	III	III	III	
10	IV	IV	IV	*Ph. pratense* 25
10	V	V	V	*T. repens* 10
10	VI	VI	VI	*Cynosurus cristatus* 20
10	VII	VII	VII	*C. cristatus* 10, *Festuca ovina* 10
10	VIII	VIII	VIII	*F. ovina* 20

During the following seasons (1929–1933) series A and B were closely cut each week, while series C was allowed to grow undisturbed. Throughout the course of the experiment natural seeding of plantains was prevented by the periodic removal of ripening scapes.

Establishment and subsequent elimination of plantains

Year 1929. In April the number of plantains occurring in each of the eight plots of the three series was determined. Before recording the plant counts a border of 20 sq. ft. round each plot was discarded, leaving an area of 4×4 ft. which was then divided into sixteen equal parts. The numbers per square foot were recorded separately. The plot counts expressed as percentages of the number of *viable* seeds sown are given in Table VII, cols. 2–4. It was found that no statistically significant differences occurred between equivalent plots for the two series A and C sown with a nurse crop. The data for these two series have therefore been combined in Table VIII, col. 2. This

table shows that when the combined series AC is compared with the no-nurse-crop series B the only significant difference (differences exceeding three times their errors) occurring between equivalent plots are those between the thinly sown I plots and between the *Trifolium repens* plots (V). The absence of a cover crop in the B series allowed the clover to grow much more vigorously. Similarly within a series

TABLE VII. *Establishment and subsequent elimination in the series A, B and C*

	Plants established % 1929			Plants eliminated (%) between the years						
				1929–31		1931–34		1929–34		
Plots	A	B	C	A	B	A	B	A	B	C
I	7	3	10	78	76	100	100	100	100	100
II	10	14	11	64	76	98	83	96	96	100
III	14	16	14	86	86	44	70	92	96	100
IV	20	22	23	5	0	3	28	8	28	80
V	9	3	10	74	98	74	100	93	100	100
VI	28	22	26	23	24	7	19	28	38	78
VII	32	27	31	25	14	0	0	25	14	56
VIII	33	28	30	14	7	0	0	14	7	38

TABLE VIII. *Mean number of plantains per sq. ft.*

	Year 1929			Year 1931			D/E_d 1929–31	
Plots	AC	B	D/E_d	A	B	D/E_d	AC and A	B and B
I	2·7 ± 0·26	1·1 ± 0·20	4·9	0·5 ± 0·15	0·0 ± —	—	6·6	—
II	5·5 ± 0·46	7·7 ± 0·77	2·5	1·8 ± 0·28	1·9 ± 0·36	0·2	6·9	6·8
III	12·3 ± 0·63	13·3 ± 1·24	0·7	1·7 ± 0·29	1·9 ± 0·28	0·5	15·3	9·0
IV	18·3 ± 1·77	18·4 ± 1·54	0·4	16·2 ± 1·04	19·3 ± 1·07	2·1	1·0	0·5
V	7·8 ± 0·66	2·9 ± 0·70	5·1	1·9 ± 0·32	0·1 ± —	—	8·0	—
VI	23·3 ± 1·20	18·6 ± 1·58	2·4	18·7 ± 0·79	14·1 ± 0·90	3·8	3·2	2·5
VII	26·9 ± 1·45	23·1 ± 1·94	1·6	20·8 ± 1·08	20·0 ± 0·80	0·6	3·4	1·5
VIII	26·5 ± 1·75	24·0 ± 1·54	1·1	23·9 ± 0·77	22·4 ± 0·82	1·3	1·4	0·9

the percentage establishment of sea plantains has been appreciably affected by the relative abundance of *T. repens*. For example, the clover plots III and V of the AC series contained significantly fewer plantains than the remaining plots which received the same quantity of plantain seed. Moreover plot V with the greatest seeding of clover possessed the lowest number of plantains. The figures for plots IV, VI, VII and VIII do not differ significantly from each other. In the B series plot V alone is distinctive, plot III having this time a count statistically similar to plots IV and VI. As in the AC series plots IV, VI, VII and VIII do not attain a significant difference.

Year 1931. This year the plantains in the C series were not counted, as accurate figures could not be obtained owing to the height of the herbage. The two mown series A and B, however, were

again examined and it was found that during this 2-year period elimination of plantains had taken place. From Table VIII it can be seen that the reduction in numbers is parallel in both series and also, from the last two columns of the same table, that in the majority of plots the reduction is statistically significant. Plots III and V have suffered a significantly greater elimination than plots IV, VI, VII and VIII. Since 1929 the clover in plots III had developed rapidly and the difference in number of plantains between these plots and plots V is no longer significant. In Table VII the relative rate of plantain elimination for the various plots since 1929 is given, the number of plantains eliminated being expressed as percentages of the number established in April 1929.

Year 1934. In April 1934 it was no longer possible to determine the number of plantains in the plots by a surface examination owing to the density of the herbage. The counts were, therefore, obtained by digging the plots and separating the plantains from the other vegetation. An examination of the plants showed that the effect of the continual cutting of the AB series had been greatly to reduce the above ground parts, and also to reduce the root length by approximately 30% and the root diameter by 20% in comparison with the unmown plots. As counts per square foot were no longer practicable, the differences in numbers between the series A, B and C and between their component plots cannot, in this instance, be assessed with statistical accuracy. Nevertheless the differences between the counts recorded per plot in 1934 and the numbers per plot surviving in the years 1931 and 1929 provide a guide to the course of elimination, and they have been expressed in percentage form in Table VII. During the last 3-year period the rate of elimination in series A and B had not been retarded appreciably as far as the clover plots were concerned. On the other hand elimination had either ceased or had been maintained at a low level in the plots IV, VI, VII and VIII.

Besides the data for the mown series AB, the 1934 records provide information relative to the uncut series C. From Table VII it will be seen that in the clover plots the elimination of plantains is complete in the unmown series C and almost complete in the mown. In the grass plots, however, the rate of elimination in the C series greatly exceeds that in the AB series.

These results may be summarized briefly as follows: (1) establishment in no case exceeded 33% of the viable seeds sown, (2) elimination was not limited to the seedling stage, (3) rate of elimination was influenced by environment.

To determine whether this elimination of plantains had been selective or merely at random, samples from equivalent plots were compared. Only plots VII and VIII contained a sufficient number of plants for a test, and the former were chosen. Eighty plants were taken at random from plots VII C and VII B respectively and each group was seeded in isolation. The remaining plants from both plots were kept until the spring of 1935 when single cuttings of equal size were taken off 102 plants from each plot. These cuttings together with 102 seedlings raised from each isolation, making a total of 408 plants, were transplanted into the garden for examination in 1936. A sample of the original seed sown on the plots in 1928, which was to have acted as a control, failed to germinate.

As size and growth habit differences were the characters which, in the wild, distinguished the grazed populations from the ungrazed, these characters were chosen in making a comparison of the material from the plots.

TABLE IX

	Plants from			Progeny of plants from		
Character	Plot VII (B)	Plot VII (C)	D/E_d	Plot VII (B)	Plot VII (C)	D/E_d
LfH	4·22 ± 0·126	4·52 ± 0·130	1·69	3·96 ± 0·099	4·59 ± 0·130	3·91
LfL	25·07 ± 0·456	25·25 ± 0·380	0·30	24·33 ± 0·416	25·21 ± 0·515	1·33
ScH	14·60 ± 0·238	14·96 ± 0·246	1·05	14·23 ± 0·268	14·92 ± 0·249	1·88
ScL	39·86 ± 0·536	40·32 ± 0·513	0·62	39·74 ± 0·560	40·82 ± 0·542	1·39
SpL	9·72 ± 0·177	10·13 ± 0·188	1·59	9·75 ± 0·170	9·99 ± 0·144	1·06
ScS/H	1·25 ± 0·027	1·22 ± 0·025	0·83	1·32 ± 0·029	1·28 ± 0·021	1·25

The results of the garden tests which are presented in Table IX show that in all the characters studied there is a slight though insignificant tendency for the plants of series C origin to be larger and more erect than those of series B origin. Furthermore, the progeny tests provide corroborative evidence of this tendency. Considering that the elimination which occurred in the unmown plot was four times as great as that in the mown, this negligible effect of the environment is somewhat surprising. It would appear from these data, therefore, that in spite of a differential death-rate the elimination of growth-forms has been predominantly at random, After 6 years it might have been expected that the differences between the two series would have been greater if the vegetative phase of the individual plants had been subject to the environmental selection imposed upon it. A conclusion that may reasonably be drawn is that since in the material employed the vegetative phase was not particularly sensitive to the imposed conditions, population differentiation in "wild" grazed and ungrazed habitats is mainly the result of

differences in the amount of seed produced by the different growth-forms, e.g. decumbent scapes would suffer less than erect ones from the attacks of grazing animals. The plan of the present experiment did not allow of this assumption being put to the test.

Breeding experiments have shown that, in both the growth-habit and size characters, populations respond rapidly to rigorous artificial selection. Unfortunately the plantain material employed in these experiments was accidentally destroyed before the records could be completed. However, the results of a parallel series of experiments with two habitat samples of diploid *Phleum pratense* are available. The components of these two samples, spaced at 2 ft. intervals, were examined during their second season, and two pairs of similar phenotypes, representing extreme variates in respect of growth-habit, i.e. decumbents and erects, were selected from each sample. These pairs were crossed *inter se* under control and their progenies were in turn examined in their second summer. From these, pairs of decumbent plants were selected from the decumbent progenies and erects from erects, and these also were crossed *inter se*. This procedure was repeated and the results are presented in Table X. It will be seen that the mean values of the first generations differ very appreciably from those of the habitat samples.

When two phenotypes, one from each of the extreme progenies derived from the second habitat samples, were crossed, the resulting population possessed values in respect of panicle height and the ratio panicle height : spread approximately midway between the parent populations, the respective values being $23{\cdot}25 \pm 0{\cdot}112$ and $1{\cdot}54 \pm 0{\cdot}011$. The cross decumbent × erect and the reciprocal yielded similar results.

TABLE X. *Rate of differentiation following rigorous phenotypic selection within two habitat samples*

Character	Sample	Decumbent selections: Third gen.	Decumbent selections: First gen.	Habitat samples	Erect selections: First gen.	Erect selections: Third gen.
Mean values:						
PH	1	$10{\cdot}8 \pm 0{\cdot}25$	$11{\cdot}7 \pm 0{\cdot}27$	$14{\cdot}0 \pm 0{\cdot}18$	$22{\cdot}6 \pm 0{\cdot}17$	$22{\cdot}3 \pm 0{\cdot}22$
	2	—	$11{\cdot}7 \pm 0{\cdot}22$	$19{\cdot}4 \pm 0{\cdot}28$	$28{\cdot}1 \pm 0{\cdot}27$	$28{\cdot}7 \pm 0{\cdot}15$
PH/S	1	$0{\cdot}3 \pm 0{\cdot}01$	$0{\cdot}7 \pm 0{\cdot}02$	$1{\cdot}1 \pm 0{\cdot}03$	$1{\cdot}9 \pm 0{\cdot}01$	$1{\cdot}9 \pm 0{\cdot}03$
	2	—	$0{\cdot}4 \pm 0{\cdot}01$	$1{\cdot}3 \pm 0{\cdot}03$	$2{\cdot}1 \pm 0{\cdot}03$	$2{\cdot}8 \pm 0{\cdot}02$
Coefficient of variation:						
PH	1	$18{\cdot}8 \pm 1{\cdot}69$	$24{\cdot}9 \pm 1{\cdot}68$	$16{\cdot}6 \pm 0{\cdot}94$	$7{\cdot}4 \pm 0{\cdot}52$	$11{\cdot}7 \pm 0{\cdot}71$
	2	—	$18{\cdot}9 \pm 1{\cdot}41$	$16{\cdot}8 \pm 1{\cdot}05$	$9{\cdot}7 \pm 0{\cdot}69$	$7{\cdot}5 \pm 0{\cdot}39$
PH/S	1	$25{\cdot}2 \pm 2{\cdot}33$	$30{\cdot}0 \pm 2{\cdot}08$	$40{\cdot}0 \pm 2{\cdot}58$	$13{\cdot}0 \pm 0{\cdot}93$	$15{\cdot}4 \pm 0{\cdot}94$
	2	—	$19{\cdot}1 \pm 1{\cdot}43$	$29{\cdot}2 \pm 1{\cdot}91$	$13{\cdot}4 \pm 0{\cdot}97$	$10{\cdot}1 \pm 0{\cdot}53$

PH = panicle height in inches.
PH/S = panicle height/spread.

V. Discussion

Initial differentiation of populations

The differences between plantain populations have been shown to be almost exclusively dependent on the frequency with which certain expressions of quantitative characters belonging to continuously graded series are represented. This lack of discontinuity makes it necessary to assess differences in terms of character mean values, and it is helpful before discussing problems of classification to consider some of the agencies responsible for altering these values.

From an examination of habitat populations in the wild, it would appear that the variety of hereditary forms constituting a population is to some extent masked by the reaction of the population as a whole to external environmental stimuli. While such fluctuating variability often exaggerates the precision of adaptation, it must actually permit the reproduction of variates whose potential values deviate from the reproductive optimum of the population. At the same time, ability on the part of variates to fluctuate in response to habitat conditions must add considerably to the stability of populations by preventing temporary changes of environment from affecting permanently their hereditary constitution. It has been demonstrated, particularly in the case of the continuously distributed coastal populations, that persistent environmental differences influence the distribution of certain hereditary characters, e.g. growth-habit and size. But it is difficult to determine to what extent ecological barriers of this kind interfere with the *dispersal* of the genetic factors responsible for the appearance of these and other characters. From the fact that the expression of certain characters such as leaf colour is often similar in adjoining habitats and that pollen from one habitat must sometimes invade another, it may be inferred that the isolation afforded by virtue of habitat differences alone is not absolute. Such incomplete isolation, while tending to decrease the degree of differentiation between populations for some non-adaptational characters, may actually increase the divergence in respect of others. For example, where physical or biotic environmental selection is in the direction of either tallness or dwarfness, the occasional acquisition from other habitats of genes inducing greater height or more extreme decumbency would facilitate a still greater differentiation between populations, under the influence of Natural Selection.

Nevertheless, in spite of the opportunities afforded the non-adaptational characters to spread under strictly ecologically main-

tained isolation, many coastal populations exhibit a marked individuality in respect of characters which have no apparent ecological significance. In coastal regions, habitats are continually being destroyed and new ones created, and the colonization of the latter introduces the possibility that some degree of spatial isolation during the process affects the distribution of non-adaptational characters. The colonization of recently formed habitats can, however, be best observed in inland districts. The trend of inland migration, as pointed out previously, is primarily from mountain habitats into small areas on the borders of streams and paths, i.e. into recently formed and more or less isolated and unoccupied habitats. Bearing in mind the heterogeneous nature of the average population, it is highly improbable that populations resulting from the sporadic invasions of habitats by a few seeds from a single locus would represent the genetic constitution of the parent population, or even be themselves of similar constitution. So long as random elimination of variates remained at zero, the introduced "neutral" genes would in all probability increase numerically at their original frequencies, provided that they were equally free of interference from those responsible for differential reproductive rates. But as a habitat reached its maximum complement random elimination would become increasingly severe and, judging by the rarity of seedlings in fully occupied habitats, seed from variates of low frequency would stand a poor chance of establishment. Thus migration followed by random elimination may play its part in establishing in a comparatively short space of time distinctions of no adaptational consequence.

Similar hereditary expressions of growth-habit and of size may be found dominating dissimilar habitats under certain circumstances, although, as has been shown, the distributions of these characters are susceptible to environmental control. For example, sample PMN 16 was collected from a habitat lying at an elevation of 100 ft. at the base of Ben Cruachan. This habitat supported a population composed of plants phenotypically almost twice the size of those occupying the upper slopes of the mountain. But when samples from both situations were grown under similar conditions in the experimental garden the size difference was no longer evident, a circumstance which suggests the absence of certain size factors in this locality.

The availability of characters is doubtless a potent force in determining the extent to which ecological differentiation is realized in isolated regions. For example, decumbent growth-habit might

conceivably dominate a sheltered ungrazed situation if by chance it was the only growth-type available, although normally its ecological importance is greatest under conditions of extreme exposure and heavy grazing. If, as appears certain, the majority of the present lowland populations represent isolated parts of long established, presumably previously selected mountain populations, it is not surprising that the differentiation of ecologically sensitive characters is less noticeable in the inland habitats than in the coastal regions where habitat contacts increase the chances of populations acquiring genes from elsewhere. By way of illustration *Saxifraga* (*Bergenia*) *crassifolia* L., which "grows copiously" at low levels in the Altai mountains and "is found as scattered individuals in sheltered places even up to the tree limit", maintains its *lowland* characteristics at the high altitudes (Turesson, 1931, p. 338). On the other hand, an alpine type of *Solidago virgaurea* L. "is found in *regio alpina* of the East-Altaian mountains, differing in regard to height and earliness from the lowland type of the same region, while in the Alps and Carpathians no such alpine type has been found" (p. 345). Turesson concludes that this "is no doubt due to the absence in these regions of the biotypes necessary for the differentiation of that type" (p. 345). Such distributional anomalies indicate the need for care in assigning an adaptive value to any character.

Classification of local differentiation

It has never been seriously suggested that all the discernible differences between individual plants should be named. However, the naming of every discernibly differentiated sea plantain population would be as unjustifiable as the naming of differences between their component plants, because few populations are identical in composition. If as Cockayne & Allen (1927, p. 259) say "the goal of taxonomy is the power to discover the status of the individual plant", the units of taxonomy would require to be determined at a level more distinctly demarcated than that at which the initial differentiation recorded in this paper takes place. Considering the nature of the differentiation of the plantain populations in Britain it would indeed be difficult to assign with any degree of accuracy an individual specimen to its appropriate population, e.g. individual specimens possessing common characteristics may occur in populations which are dissimilar by virtue of their constituents being represented in different proportions. Of the thirty-two samples examined from habitats in Britain, all except three possessed decumbent growth

forms, distinguished by having the scapes peripheral and decumbent, only five contained truly erect types, and all contained forms intermediate between these two extremes. When, however, the local distribution of growth-habit was examined it was found that the local population differences were not necessarily associated with the presence of peculiar growth-forms but were due to changes in the numerical relationships between types. Moreover, the examination of the hereditary composition of population samples from certain recognizably different habitats demonstrated that in respect of the continuously graded character series, growth-habit and size, this local differentiation is effected in response to local environmental conditions. Plants with peripheral and decumbent scapes can be readily distinguished from those which have scapes erect and general. If these forms had occurred in each local habitat in unvarying proportions, it might have been sufficient only to record their existence. In reality, however, it is necessary to consider not only the proportional distribution of these extreme forms of the character series, but also the effects of ecological conditions upon the distribution of the series as a whole. When it is found that the characters which differentiate one population from another belong to a continuous unbroken series, any attempt to describe the population differences verbally in terms of such characters naturally tends towards an arbitrary description of the more or less recognizable steps within the series. But since all the components of a series are presumably liable to be acted upon by Natural Selection, an artificial grouping within the series might conceivably be detrimental to the proper interpretation of the forces operative in Nature. The accuracy of recording the distribution of the variates belonging to a continuous series can be greatly increased by recording their presence in numerical terms either by the direct measurement of the characters of the individual variates, e.g. as in assessing the character scape spread : height ratio, or by devising a numerical scale for the recording of observable but ill-definable differences, e.g. the evaluation of habit grade.

In addition to the differentiation of populations accounted for by the uneven representation of ecologically controlled characters, qualitative differences are also to be found. Such qualitative differences as the presence or absence of spots and hairs on the leaves fall within this category, but in reality they merely represent definable steps in quantitative series, e.g. the difference between glabrous leaves and those exhibiting a few hairs being very slight indeed. Similarly the absence of the leaf spot character represents the end-point of a

series culminating at the other extreme in the coalescence of numerous deeply pigmented spots. The distribution of spotted-leaved plants is apparently independent of ecological selection although the frequency of spotted plants varies much locally. The data previously given show that some habitat samples may entirely lack spotted plants, e.g. PMN 55 from a spatially isolated population; this, and not the fact that plants can be separated into spotted and non-spotted categories, is an important taxonomic observation from the evolutionary standpoint.

Here then is the initial population differentiation resulting from the operation of different causes; in the case of the growth-habit and size characters it is in response to environmental conditions, and in that of leaf spot apparently it is in consequence of chance spatial isolation of non-spotted plants. Since the criterion for delimiting habitat populations rests mainly on the differential numerical representations of characters, no clear-cut morphological distinction exists between habitat populations. However, on the basis of the Natural Selection theory the degree of morphological distinctness should be greatest as the ecological differences influencing the distribution of the characters become more pronounced. On the other hand, the character differentiation resulting from the chance isolation of a part of a larger population may also vary considerably in degree and may perhaps be greater, even from its inception, than the differences between many ecologically isolated populations. For example, the lack of spotted-leaved plants in a habitat is more striking than is a difference of, say, a few centimetres in scape length. In an intrafertile assemblage, any character difference which indicates the process by which populations in the wild maintain their identity can be justifiably regarded as being of at least as great value in an experimental taxonomic system as the degree of morphological distinctness. In other words, when dealing with such dynamic units as local populations the process of differentiation is of more importance taxonomically than the degree of discernible morphological differences exhibited at any given time. The units of experimental taxonomy, if they are to represent the natural subdivisions of a wild population, will therefore require to be based on the causes which initiate differentiation rather than on the extent of the observable differences between populations. That is, the character differences will be diagnostic of populations belonging to the same taxonomic unit but will not be the determinants of taxonomic status.

If names are to be given for reference purposes to different populations of the same taxonomic status the question arises whether (1) distinctive habitat populations should each receive a name indicative of the habitat, or (2) the names of different populations should have reference to the proportional representation of one or more ecological indicator characters, e.g. growth-habit. In the first case the greater the habitat diversification the greater would be the need for names, e.g. the five coastal groups of habitat populations studied, and probably many more, would be eligible; in the second the number would be constant because all the differences between the habitat populations could be recorded in terms of the three most easily recognizable growth-habit types. Although plant size also follows an ecological sequence, growth-habit is to be preferred as a basis for the nomenclature because it can be identified with considerable accuracy without recourse to actual measurement.

Using Turesson's (1922) terminology, the ecologically differentiated races of *Plantago maritima* within Britain can be classified according to the predominating type of growth-habit into three ecotypes, *decumbens*, *ascendens* and *erecta*. The diagnostic characters are represented diagramatically in Fig. 3, which also depicts the relationship between the largest and smallest form of each growth-type.

The relationship between the named ecotypes and the populations occupying the Inland habitats and the habitat categories (*a*) to (*e*) is given in Fig. 4. The position of the populations on the habit grade scale and the size relationships of their component plants are based on the mean values for the characters habit grade and scape volume given in Table I.

There still remains the population (PMN 55) which lacks the leaf-spot character. As the spotted condition is almost universally distributed in Britain regardless of ecological differences, its lack is presumed to be due to the chance introduction of recessive plants into this spatially isolated habitat. Since population differentiation of this kind is not ecotypic, units separated in this manner should not be confused with ecotypes. It is therefore proposed to give this population the taxonomic status of a geo-ecotype (Gregor 1931) and apply the name *immaculata*.

Ecotypes of the same species situated in different regions are, however, likely to exhibit differences due to an uneven geographical distribution of ecologically tolerant characters. Even in a region the size of Britain there is evidence that on the average the Inland

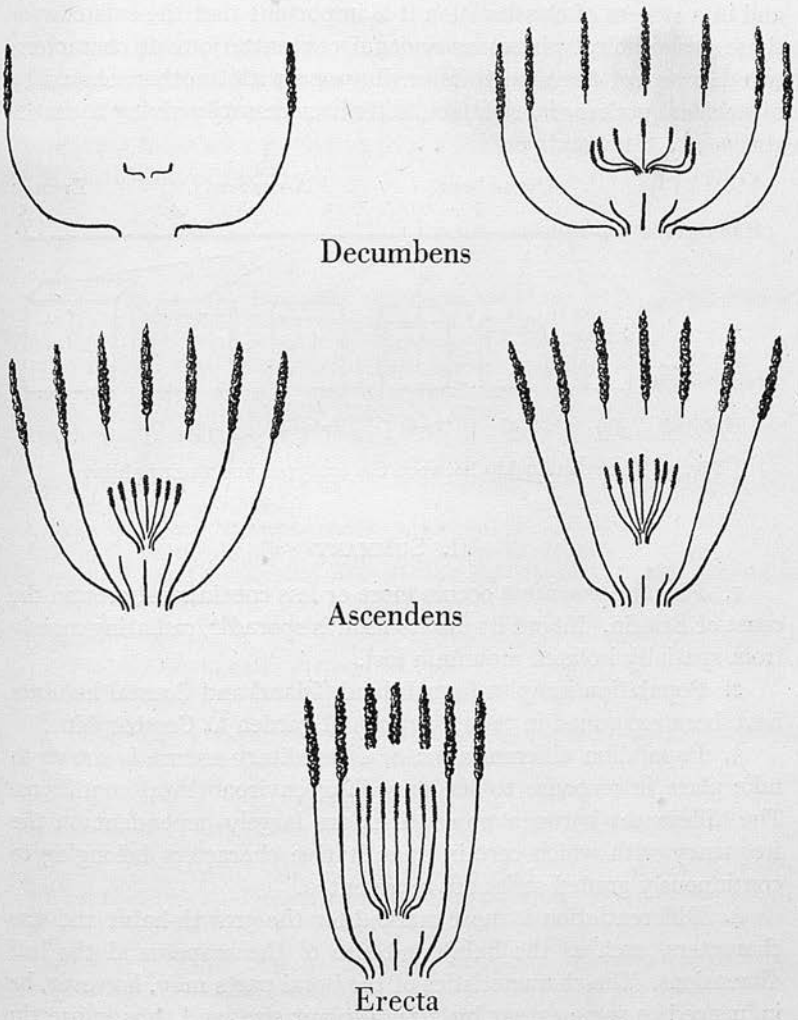

Fig. 3. Ecotypes of *Plantago maritima*.

ecotypes have sepals which are narrower in proportion to their length than those of the Coastal populations (Table I). Moreover the Coastal populations of the Mainland are less hairy than the ones from the Hebridean Islands (Table III). Geographical restriction of this kind affects the characters of all the ecotypes within the area concerned, and in a system of classification it is important that the existence of these geographical phases or regional concentrations of characters, whether or not they merge insensibly one with another, should be mentioned, perhaps in a preface, without necessarily giving them the status of a taxonomic unit.

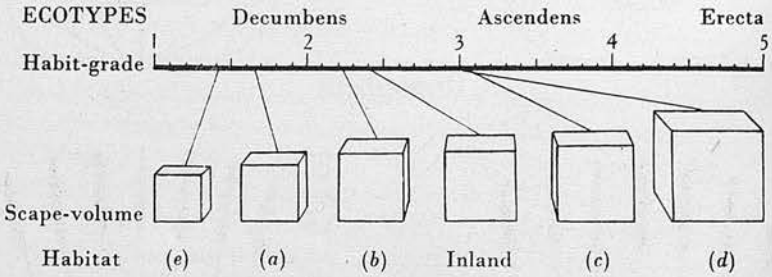

Fig. 4. The relationship between the ecotypes and their habitats.

VI. SUMMARY

1. *Plantago maritima* occurs more or less continuously round the coast of Britain. Inland its distribution is sporadic, radiating mainly from spatially isolated mountain loci.

2. Population samples from Inland, Island and Coastal habitats have been examined in the experimental garden at Corstorphine.

3. Population differentiation of a hereditary nature is shown to take place in response to the prevailing environmental conditions. The differences between populations are largely dependent on the frequency with which certain quantitative characters belonging to continuously graded series are represented.

4. Differentiation is most marked for the growth-habit and size characters, such as the habit and size of the scapes and the leaf dimensions. The characteristics of the floral parts may, however, be influenced to some extent by general plant size, and thus indirectly by habitat conditions.

5. It is suggested that in classifying races emphasis should be transferred from the degree of morphological distinctness exhibited by populations to the processes which initiate differentiation, and

that taxonomic *status* should be accorded the units which are maintained by particular natural circumstances irrespective of the extent to which they differ morphologically.

6. Three ecotypes, *decumbens*, *ascendens* and *erecta*, and one geoecotype, *immaculata*, have been named.

I am greatly indebted to my colleague Mr J. M. S. Lang for helping me to collect the data from which the foregoing conclusions have been drawn, and to Prof. J. R. Matthews of Aberdeen, for supplying information relative to the distribution of *Ph. maritima* in the north-east of Scotland.

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EXPERIMENTAL TAXONOMY.

IV. Population differentiation in N. American and European Sea Plantains allied to *Plantago maritima* L.

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C O N T E N T S.

INTRODUCTION.

The present investigation is primarily concerned with the racial divergence within the diploid population of Sea Plantains allied to P. maritima L., and is based on the detailed study in an experimental garden of representative samples of some of its very numerous more or less "self-contained" breeding communities. Breeding communities are the small populations whose members are likely to breed more often amongst themselves than with members of neighbouring colonies. In culture the separate samples have been found almost invariably to possess an individuality of their own; an individuality which is often only perceptible by the majority of individuals in a sample resembling each other more than they resemble the majority of individuals of another sample. The differences however cannot always be expressed in terms of variates possessed by one sample and not by another. Nevertheless within the total population the unequal distribution of certain characters makes it possible to detect communities possessing attributes peculiar to themselves. But since the territories covered by such distinctive characters are seldom entirely coincident the chances of identifying populations by an association of these

attributes in relatively stable combination is not too great.

The customary practice of according taxonomic recognition only to those populations which show a relatively high degree of association (fortuitous and otherwise) involving several "diagnostic" characters, would tend to obscure the geographical and ecological relationships of individual characters and character variations. By such treatment populations of considerable evolutionary consequence might even fail to find a place in the taxonomic scheme, e.g. an ecological race exhibiting a low degree of character association which extends through the territories occupied by two or more populations of high character association, or populations which are separated by sterility barriers unaccompanied by appreciable morphological divergence. It is just such anomalies as these which tend to focus attention on the apparent artificiality of orthodox taxonomy. But as Gilmour (1937) has pointed out in a valuable article on the logic of classification"it is usually stated in logic that a system of classification is the more natural the more propositions there are that can be made regarding the classes". Judged then by this standard

most biologists will agree that the present morphological classification of organisms is the most "natural" one yet devised. And as the difference between a natural and an artificial classification is only one of degree, the incorporation of additional data into the traditional system could only result in raising its degree of naturalness. Nevertheless, until more is known of the specific and infra-specific categories of variation in the wild, a too precipit~~eus~~ate amalgamation of experimental and traditional taxonomy would almost inevitably have repercussions detrimental to the present usefulness of the established morphological system. Therefore in the meantime it would seem more appropriate for experimental taxonomists to refrain from attempting to meet their requirements by any redefinition of the orthodox classificatory categories, but instead to use a complementary system of classification with a distinctive terminology, at least until the true value of new categories, and their possible place in a more comprehensive system, can be assessed. Whether or not intensive experimental study of populations will of itself lead ultimately to a classification more natural (in the sense of Gilmour) than the existing one cannot be foreseen, but there is little doubt that an additional source of

classified data relative to the constitution of species-segregates will have its value.

The present investigation has involved the examination of living material in the experimental garden at Corstorphine. The collection of seed samples from various habitats, the subsequent cultivation of populations and the sampling of individual plants were carried out in accordance with the methods found by preliminary experimentation to be the most reliable. These methods have already been described (Gregor, Davey & Lang, 1936, pp.327-8). Briefly the technique was as follows:- Ripe spikes were systematically gathered from comparatively well-defined but not necessarily spatially isolated habitats: seeds were sown in weed-free soil and later 102 seedlings of each sample were transplanted into the experimental garden where they were examined in their second year. Every plant received a number, and the data relating to each were recorded. A list of the samples is given in Table I.

TABLE I. Source of Material

Ref. No.	Locality	Habitat Notes	Date Collected	Collector
	N. AMERICA, West Coast.			
56	Montaro lighthouse, California.	Ocean bluff; granitic soil; competition.	14.11.30	Prof. Leroy Abrams.
57	do. do.	Ocean bluff; granitic soil; no competition.	14.11.30	do.
58	do. do.	Road excavation; granitic soil; no competition.	14.11.30	do.
85	Salado, California.	Coastal dunes.	23.10.32	Dr. J. Clausen.
86	Sitka, Alaska		-. -.32	Dr. Eric Hulten.
	East Coast.			
59	Charlottetown, Prince Edward Island.	Swamp at seaside.	22. 9.31	per Dr. O. McConkey.
60	Margertsville, Nova Scotia.	Rocky cliffs, Bay of Fundy Shore.	22. 9.31	Mr. J. F. Hookey.
61	Hortonville, Nova Scotia.	Just about high tide line, meadow dykeland.	21. 9.31	do.
73	Clondorme, Gaspe County, P.Q.		25. 7.32	Mr. J. Rausseau.
81	Scituate, Mass.	Salt marsh.	11.10.32	Mr. C. A. Weatherby.
82	Momauguin, New Haven, Conn.	Salt marsh.	14. 9.32	J. W. G.
83	Point of Pines, Boston, Mass.	Salt marsh.	12. 9.32	do.
84	Gloucester, Mass.	Rocks by the sea.	16.10.32	Mr. C. A. Weatherby.
89	Bar Harbor, Me.	Maritime rocks.	15. 7.34	Dr. G. G. Hahn.
	GREENLAND			
52	Godhavn, W. Greenland.	Gneiss cliffs (coastal).	25. 9.30	Mr. M. P. Porsild.
	N. EUROPE, Iceland.			
66	Reyjavik.		30. 7.30	per Mr. C. Rasmussen.
93	Isafjordur (N.W.).	Maritime rocks and gravel, above high tide line.	8. 9.35	J. W. G.
94	Midfjordur (N.W.).	10 Km. inland, stony soil thinly populated.	12. 9.35	do.
95	Saurbaer (W.).	1 Km. inland, stony hillside.	13. 9.35	do.
96	Reykjavik.	Turf hummocks, from high tide line to 100 yards inland.	14. 9.35	do.
97	Hafnarfjordur (W.).	Rocky hill (coastal).	7. 9.35	do.
98	Stadur (S.W.).	A rift in lava containing fresh water.	20. 9.35	do.
99	Reykjanes (S.W.).	Pasture on lava soil.	20. 9.35	do.
100	Reykjanes (S.W.).	Vicinity of hot spring "Geysir".	20. 9.35	do.
102	Reykir (S.).	Neighbourhood of "Gryta" geysir.	5. 9.35	do.
103	Great Geysir.	Neighbourhood of Great Geysir.	5. 9.35	do.
104	Hlidarendi (S.).	Gravelly river bed 22 Km. inland.	16. 9.35	do.
105	Mulakot (S.).	Rocky hillside, 350 feet above sea level.	16. 9.35	do.
106	Skogafoss (S.).	Gravelly river bed.	18. 9.35	do.
107	Portland (S.).	Exposed cliff top.	19. 9.35	do.
108	Vik (S.).	Sandy rock ledges (coastal).	19. 9.35	do.
109	Solheimajökull (S.).	Almost unpopulated moraines close to glacier.	18. 9.35	do.
	Faroes.			
51	Højvig, Thorshavn.	Maritime rocks.	25. 8.30	Mr. E. Knudsen.
110	Thorshavn	Maritime rocks.	2. 9.35	J. W. G.
	Britain.	Thirty-three localities (see GREGOR, 1938).		
	Norway.			
114	Svolvaer, Lofoten Islands.	Coastal mud at tide mark.	3. 7.38	J. W. G.

TABLE III. Variate Ranges (Summary) see Table II. For full character headings

Region	HbG.	ScS : H.	ScS. in.	ScH. in.	ScL. cm.	ScTh. mm.	SpL. cm.	ScV. litres	LfL. cm.	LfB. mm.	LfIx.	LfTh. mm.	LfS. in.	LfH. in.	LfS : H.	SpD.
N. America	1 - 5	0.4 - 3.3	4 - 22	3 - 17	11 - 42	1.0 - 2.8	4 - 16	0.1 - 5.3	6 - 32	3 - 19	6 - 65	0.5 - 1.8	1 - 16	1.0 - 5.5	1.0 - 7.0	6 - 21
N. Europe	1 - 5	0.5 - 7.1	3 - 31	1 - 29	5 - 69	0.7 - 3.5	1 - 21	0.1 - 20.4	3 - 56	1 - 22	13 - 100	0.5 - 2.0	1 - 28	0.5 - 13.0	1.0 - 9.0	7 - 23
Alps	2 - 3	1.0 - 1.9	6 - 17	5 - 11	9 - 26	1.0 - 2.1	2 - 6	0.2 - 2.3	5 - 16	4 - 12	8 - 28	0.5 - 1.0	5 - 14	2.0 - 5.5	1.9 - 3.7	12 - 25
Sub-region																
W. America	1 - 3	1.0 - 3.3	6 - 21	3 - 13	11 - 38	1.0 - 2.8	4 - 14	0.1 - 3.8	6 - 29	3 - 19	6 - 50	0.5 - 1.8	1 - 11	1.0 - 3.5	1.0 - 7.0	8 - 21
E. America	1 - 5	0.4 - 1.8	4 - 22	6 - 17	20 - 42	1.0 - 2.2	4 - 16	0.1 - 5.3	12 - 32	3 - 12	19 - 65	0.6 - 1.6	4 - 16	2.0 - 5.5	1.6 - 5.3	6 - 17
Iceland	1 - 4	0.8 - 6.0	3 - 19	2 - 15	6 - 39	0.7 - 2.3	1 - 12	0.1 - 9.5	5 - 32	1 - 12	13 - 95	0.6 - 1.1	1 - 15	0.5 - 5.0	2.0 - 8.0	10 - 23
Faroes	1 - 4	1.0 - 3.5	5 - 20	2 - 13	9 - 40	0.9 - 2.1	2 - 12	0.1 - 3.8	5 - 30	2 - 10	14 - 60	0.7 - 1.4	1 - 13	1.0 - 4.5	1.1 - 5.9	10 - 20
Britain	1 - 5	0.5 - 7.1	4 - 31	1 - 27	5 - 69	0.7 - 3.5	1 - 21	0.1 - 20.4	3 - 51	1 - 22	13 - 100	0.5 - 2.0	2 - 28	1.0 - 13.0	1.0 - 9.0	7 - 21
S. Sweden	1 - 5	0.6 - 1.4	9 - 28	13 - 24	35 - 68	1.4 - 2.6	6 - 16	1.0 - 14.2	17 - 56	4 - 15	19 - 86	0.6 - 1.8	7 - 23	2.5 - 10.5	1.6 - 4.4	7 - 22

Region	BrL. mm.	BrB. mm.	BrIx.	Sep.L. mm.	Sep.B. mm.	Sep. Ix.	SdL. mm.	SdB. mm.	SdIx.	AL. mm.	ATL. mm.	BrL : SepL.	ScL : SpL.	ScL : LfL.
N. America	1.71 - 3.77	0.99 - 2.06	1.1 - 2.3	1.63 - 2.79	0.94 - 1.84	1.2 - 2.3	1.33 - 2.79	0.673 - 1.29	1.6 - 2.8	1.29 - 2.27	0.129 - 0.472	0.8 - 1.5	2.3 - 5.8	0.7 - 3.5
N. Europe	1.41 - 4.28	0.77 - 2.23	1.1 - 3.2	1.54 - 3.39	0.73 - 1.67	1.3 - 3.2	1.63 - 3.51	0.772 - 1.46	1.7 - 3.5	1.33 - 3.09	0.086 - 0.472	0.7 - 1.5	1.8 - 8.8	0.7 - 3.2
Alps	1.80 - 3.39	0.99 - 1.63	1.5 - 2.6	1.50 - 2.49	0.99 - 1.54	1.3 - 1.9	1.41 - 2.14	0.686 - 0.99	1.8 - 2.4	1.63 - 2.36	0.129 - 0.343	1.0 - 1.7	3.2 - 7.7	1.1 - 2.9
Sub-region														
W. America	1.71 - 3.39	1.20 - 2.06	1.1 - 2.0	1.63 - 2.79	1.20 - 1.54	1.2 - 1.8	1.33 - 2.66	0.772 - 1.29	1.6 - 2.5	1.50 - 2.27	0.129 - 0.386	0.8 - 1.5	2.3 - 5.0	0.7 - 3.5
E. America	1.97 - 3.77	0.99 - 1.97	1.1 - 2.3	1.76 - 3.26	0.94 - 1.84	1.3 - 2.3	1.37 - 2.79	0.673 - 1.24	1.6 - 2.8	1.29 - 2.14	0.214 - 0.472	0.9 - 1.5	2.3 - 5.8	0.9 - 1.8
Iceland	1.41 - 2.83	0.77 - 1.50	1.3 - 2.5	1.54 - 2.57	0.77 - 1.37	1.3 - 2.8	1.63 - 2.74	0.772 - 1.20	1.7 - 2.9	1.33 - 2.36	0.086 - 0.429	0.7 - 1.4	2.2 - 7.0	0.9 - 2.8
Faroes	1.50 - 2.70	0.90 - 1.67	1.3 - 2.2	1.76 - 2.70	0.90 - 1.29	1.6 - 2.9	1.80 - 2.91	0.814 - 1.24	1.7 - 2.9	1.59 - 2.91	0.171 - 0.386	0.8 - 1.2	2.8 - 5.3	0.8 - 3.2
Britain	1.50 - 4.16	0.81 - 2.14	1.1 - 3.2	1.67 - 3.39	0.90 - 1.67	1.5 - 3.2	1.63 - 3.51	0.772 - 1.46	1.8 - 3.5	1.46 - 3.09	0.086 - 0.472	0.7 - 1.5	1.8 - 8.5	0.7 - 2.8
S. Sweden	1.97 - 4.28	0.90 - 2.23	1.6 - 2.9	1.89 - 2.79	0.73 - 1.24	1.8 - 3.0	1.80 - 3.21	0.814 - 1.20	2.0 - 2.9	1.54 - 3.09	0.086 - 0.429	0.9 - 1.5	3.1 - 8.8	1.0 - 2.3

II. THE ANALYSIS OF MEASURABLE CHARACTERS

(a) The comparison of average character values.

In Table II the mean values are given for the various characters of the samples examined, while in Table III the variate ranges are given for the same characters. In both these tables the samples have been arranged according to their geographical source by regions (A) N. American, (B) N. European and (C) Alpine (from the Alps). (A) has been again sub-divided into sub-regions (a) Western N. America, and (b) Eastern N. America, and (B) into (a) Iceland, (b) Faroes, (c) Britain and (d) South Sweden. Several samples represented by relatively few individuals have been omitted from Tables II and III.

When making comparisons between any two of these regions or sub-regions an average character value cannot be usefully employed for all characters. For example it will be found that three out of the four samples from Western America are derived from somewhat similar habitats in California, and since growth-habit and the size of organs have been shown to be influenced by ecological conditions (Gregor, 1938), the average of the mean values for these characters is probably biassed by the predominance of Californian samples. There are, however,

other characters, e.g. anther length, which, being less influenced by ecological conditions, vary locally in a more or less random fashion. These characters have therefore been chosen as the most reliable indicators of average regional differentiation. Since the sub-regional means differ considerably and since these means are based on unequal numbers of samples, the regional averages are liable to be biassed in favour of the sub-region supplying the greatest number of samples. For example in N. Europe the British samples outnumber those from any other country and in consequence the North European average reflects this excess. By using the method of analysis of variance, analysing the mean variability into portions attributable to regions and sub-regions, it is possible to overcome this bias to some extent, and significant differences between regions and between sub-regions have been proved to exist. The 1 per cent level of the distribution of Z (Fisher, 1932, Table VI.) has been taken as the criterion of significance.

It will be seen from Table IV that the American samples differ from the North European for the characters bract, sepal and seed indices, anther length and scape length : spike length. Therefore, although, as will be seen from Table II, the regional mean ranges are

TABLE IV. The comparison of regional average values.

CHARACTER	REGIONS		SUB-REGIONS					
	N.America	N.Europe	W.America	E.America	Iceland	Faroes	Britain	S.Sweden
Seed Index	2.06*	2.44	1.92	2.17	2.29	2.26	2.49	2.40
Bract Index	1.61*	1.93	1.54	1.66	1.77	1.77	1.97	2.09
Sepal Index	1.58*	2.08	1.45	1.60*	1.98	2.06	2.12	2.14
Bract L./Sepal L.	1.13	1.05	1.06	1.17*	1.00	0.98	1.07	1.08
Anther Length	1.76*	2.10	1.83	1.69	1.91	1.99	2.15	2.09
Anther Tip L.	0.28	0.27	0.25	0.31*	0.24	0.25	0.27	0.29
Scape L./Spike L.	3.33*	3.92	3.25	3.39	3.67	3.76	3.91*	4.99
Scape L./Leaf L.	1.48	1.49	1.71	1.30	1.51	1.55	1.49	1.49

* indicates a significant break between adjacent values.

continuous this analysis demonstrates that on the average the N. American samples have bracts, sepals and seeds relatively broader in proportion to length than those of N. Europe.

The analysis of variance has also shown that significant differences are to be found between sub-regions for seven out of the eight characters examined, scape length : leaf length being the exception.

In Table IV the sub-regions have been arranged in geographical sequence and the significance of the differences between adjacent average values has been determined from Fisher's table of t (Fisher, 1932, Table IV). It will be noted that, while lacking significant breaks in the series, the N. European sub-regions exhibit a tendency for the bracts and sepals to become progressively narrower in relation to length from Iceland towards South Sweden. Of the five characters for which significant differences have been established between N. America and N. Europe only one, sepal index, shows a break in the range of mean values between Atlantic America and Iceland, demonstrating that the transition from the one region to the other is more or less gradual.

(b) The comparison of the range of character mean values.

For reasons which have been already stated regarding the limited usefulness of comparisons between the regional and sub-regional average values, the ranges of the mean values have been taken as the general basis of comparison. Breaks in continuity of these ranges have been regarded as significant when the difference between the highest mean of one region or sub-region and the lowest of another exceeds three times its error; e.g. for the character scape height a break occurs between the western and eastern N. American sub-regions, the highest value for W. America is 9.4 ± 0.18 inches and the lowest for E. America is 10.5 ± 0.27 inches, a difference of 1.1 ± 0.32 inches.

American and North European samples compared: The character sepal index provides the only break between the N. American and N. European ranges of sample means, a break which is not significant. However, as Iceland is the part of Europe nearest the American Continent it is of interest to compare the range of mean values of samples for this sub-region with that for Atlantic North America. Between these two sub-regions significant gaps occur for the characters bract and sepal breadth, anther tip length and scape spread : height. Nevertheless the geographic continuity of all these characters is preserved by the

overlapping of the variate ranges, as may be seen by reference to Table III.

American samples compared: An examination of the mean ranges showsthat the mean values of samples from the East and West coasts overlap with the exception of those of scape length and height; scape spread : height; habit-grade; leaf length, spread and height; sepal index and anther tip length. Of these breaks, however, only those for scape height, leaf spread and height and possibly habit grade (a character for which there is no reliable error available) are statistically significant. That is, the sub-regional discontinuity is confined to measurements of growth-habit characters. But when reference is made to Table III it will be seen that the discontinuity does not extend to the variate ranges, every character exhibiting overlapping to some extent.

A glance at this table will show how evident it is that even when certain sample mean values deviate distinctly from others in respect of the same character, an individual plant might equally well belong to any one of a number of different samples. For example, the most decumbent specimens in California are no more decumbent than specimens found on the Atlantic coast, and the most upright Californian specimens have their equivalents in all the Atlantic samples. Moreover every one of the eastern

American samples contains specimens having broader leaves than the narrowest leaf forms of Western America, although on the average the Californian samples have significantly broader leaves than any samples from the East Coast.

The mean and variate range values having thus failed to provide a separation of the American sea plantains into a Pacific and an Atlantic type, it is now necessary to examine the American population as a whole and endeavour to discover whether a more localised differentiation has taken place in this area. Of all the American samples the three from California (samples 56, 57 and 58) were the most striking to the casual observer on account of their decumbent scapes and broad leaves. The mean values bear out the truth of this observation and demonstrate that, in addition to their differing from all other American samples for the characters scape spread : height and leaf breadth, they also differ significantly in respect of leaf length (short), leaf index (broad in relation to length), scape length : leaf length (leaves considerably shorter than scapes) and seed index (seeds relatively broad in relation to length).

The next most obvious difference between samples was that distinguishing samples 81 and 82 from the remainder of the American populations, these two samples being

characterised by their upright growth-habit and the relative laxity of their spikes. Again these differences are confirmed by reference to Table II where it will be found that the mean values for scape spread : height and spike density differ significantly from other American samples. With the exception of seed index (seeds relatively long in comparison to breadth) no other measurable difference of importance occurs.

Since a more dense-spiked race also occurs on the New England coast an examination is advisable of the character mean values of samples of both spike types from this restricted geographical area. If samples 81 and 82 be regarded as representative of the lax-spiked type and 84 and 89 of the more dense type, then a simultaneous comparison can be made between samples from salt marsh and maritime rock habitats. The result is that the salt marsh samples (81 and 82), in addition to having spikes more lax and scapes more erect than the maritime rock samples (84 and 89), differ significantly from the latter in that (1) their bracts and sepals, as shown by the respective indices, are broader in relation to length; (2) their seeds have greater absolute length, and are proportionately narrower; and

(3) their anthers are larger. Davey & Lang (1939) give some evidence indicative of a tendency for the bract dimensions, in particular bract breadth, to be negatively correlated with the density of the spike. Lax-spiked individuals with relatively broad bracts are, however, not peculiar to the salt-marsh habitats, as may be seen from Table III. But the fact that plants with lax spikes and plants with relatively dense spikes predominate respectively in salt marsh and maritime rock habitats provides evidence which suggests that, in respect of this character, population differentiation has occurred in response to ecological conditions. The supremacy of lax-spiked plants on other salt marshes of the Atlantic coast is also evidenced by the data obtained from samples 59, 83 and 61. Although these samples do not exceed twenty-five plants each, and therefore have not been included in the table of means, their spike density values 7.23, 7.50 and 8.33 respectively are of interest in that they are all low in comparison with the samples 84, 89 and 60 from rock habitats.

A cross between a compact-spiked plant in sample 56 from California and a lax-spiked plant from sample 81 gave an F_1 generation of 64 plants having a mean spike density value of 6.94 ± 0.200, a figure almost identical

with that of 7.0 recorded for the male parent. A population of 64 plants was also grown from seed obtained by self-pollinating the Californian female parent; this population had a spike density value of 12.70 ± 0.231. Thus in eastern America the presence of a dominant gene is apparently responsible for this lax-spike character, a character which has not been expressed to the same degree in any other region from which samples have been examined.

North European samples compared: No significant breaks in the mean value ranges occur between the sub-regions, provided the countries are taken in the geographical sequence Iceland, Faroes, Britain and South Sweden. Such continuity makes the delimitation of sharply defined regional races impossible. Nevertheless if the range of the S. Swedish samples is compared with the ranges of the samples from Iceland and the Faroes, discontinuities are to be found in many characters. These characters are those descriptive of size and growth-habit, with the exception of the bract and sepal indices and bract length : sepal length. These data suggest that maximum plant size is greater in Britain and South Sweden than it is in Iceland and the Faroes, and also that the bract and sepal indices and the ratio bract

length : sepal length reach their narrowest expression towards the south of this region. Although Britain possesses populations which exceed those of Iceland in erectness and plant size these two countries are alike in having populations of dwarf, decumbent plants, e.g. the Icelandic sample 100 and the British sample 47. Moreover, while there are British populations (sample 21) with bracts of narrower proportions than any recorded from Iceland, yet at the other extreme there is no significant difference between these sub-regions (samples 36 and 100). With the exception of scape height the variate range for North Europe is continuous.

The single Alpine sample 111 is separated significantly from all North European mean values in respect of leaf index (low), seed measurements (low seed index) and sepal index (low). However, with two minor exceptions the variate ranges for these three characters fall completely within the North European range.

III. THE ANALYSIS OF NON-MEASURABLE CHARACTERS.

(1) Leaf pubescence: The leaves were examined under a 12X lens and the distribution and density of hairs was classified into nine arbitrary grades; (1) glabrous, (2) very few scattered hairs on margins, (3) few scattered hairs on margins, (4) a considerable number of hairs on margins, (5) hairs on margins and very few scattered hairs on lower surface, (6) hairs on margins and scattered hairs on lower surface, (7) hairs on margins and scattered hairs on upper surface, (8) hairs on margins and scattered hairs on both surfaces, and (9) thinly pubescent.

Table V gives the percentage number of plants occurring in the different grades, summarised for the sub-regions. All nine grades are represented in both America and Europe. W. America, Britain and Sweden have high percentages of plants with hairs confined to the leaf margins, whereas in the majority of plants from E. America, Iceland and the Faroes, the hairs are more generally distributed over the leaf surface. By totalling the percentages for grades of maximum pubescence for the margins, lower surfaces, and both surfaces, viz. 4, 6 and 9, an idea can be obtained of

TABLE V. Leaf pubescence. Percentage plants in each grade.

Sub-regions	GRADES									Percentage plants in grades 4, 6 and 9.
	1	2	3	4	5	6	7	8	9	
W. America	0.8	22.8	30.3	21.4	12.4	9.9	1.1	1.0	0.4	31.7
E. America	0.5	8.5	7.8	2.0	9.2	5.0	2.2	23.1	41.7	48.7
Iceland	0.0	0.2	1.6	3.4	8.9	42.4	0.0	6.3	37.2	83.0
Faroes	0.0	1.1	4.7	10.6	38.2	33.2	1.0	7.1	4.2	48.2
Britain	2.8	51.3	12.2	6.2	10.2	14.0	0.8	2.8	2.3	22.5
S. Sweden	1.0	63.3	10.0	3.7	16.8	3.2	1.1	1.1	0.0	6.9
Alps (Allgäu)	0.6	17.3	7.0	3.3	38.4	23.0	0.0	10.0	0.6	29.9

TABLE VI. Density and length of leaf margin hairs.

Region	No. of hairs per 4.29 mm.		Hair length in mm.	
	Range of means	Variate range	Range of means	Variate range
E. America	2.29 - 10.68	0 - 23	0.065 - 0.22	0.043 - 0.51
N. Europe	1.35 - 13.78	0 - 24	0.095 - 0.47	0.043 - 1.46
Alps (Allgäu)	4.47 - 13.44	0 - 33	0.091 - 0.11	0.043 - 0.21

TABLE VII. Leaf tooth grade

Region	Variate Range	MEAN	Range of means
W. America	1 - 5	1.01	1.00 - 1.04
E. America	1 - 7	1.08	1.00 - 1.25
Iceland	1 - 4	1.09	1.03 - 1.26
Faroes	1 - 9	1.68	1.23 - 2.73
Britain	1 -13	1.64	1.02 - 2.81
S. Sweden	1 - 9	1.98	1.23 - 2.73
Alps (Allgäu)	1 - 9	1.54	1.50 - 1.57

the relative differences in hair density between sub-regions. By this standard of comparison the Icelandic samples are the most densely hairy, and the American samples fall within the European range. A further indication of hair density may be obtained from Table VI where the number of hairs per 4.29 mm. of the leaf margin and the lengths of the longest hairs in this distance are recorded for six samples from E. America, the same number from N. Europe and three samples from the Alps.

(2) Leaf Tooth grade: The margins of sea plantain leaves may be entire or toothed, the length of the teeth varying greatly even in a single plant. To determine sample differences for this character the longest tooth per plant, as judged by eye, was measured in mm. and the measurements recorded in grades as follows: teeth of 1 mm. or less were denoted by the figure one, teeth of 1.5 mm. by two, teeth of 2.0 mm. by three and so on. The results are given in Table VII.

(3) Leaf spot: The presence of anthocyanin leaf spots is a feature of many samples. The spots are usually small and of a deep wine-red colour and can best be observed in early spring and late autumn. The lack of spots is a recessive condition, and Dr. Black of this Institute who has grown an F_2 population of green x spotted

plants under conditions favourable to the expression of this character finds that the ratio spotted : green is as 3 : 1, (260 : 79). The frequency of spotted-leaved plants has varied widely from sample to sample even locally. The results of the observations are summarised in Table VIII and it will be noticed that while the character is present in E. America, Greenland and in all the sub-regions of North Europe, it has not been recorded from W. America or from the Alps.

TABLE VIII. Percentage frequency of spotted-leaved plants.

Sub-region	Means	Ranges
W. America	-	------
E. America	73	3 - 100
Greenland	76*	
Arctic Europe	78+	55 - 100
Iceland	72	40 - 98
Sweden	64	52 - 76
Faroes	8	4 - 12
Britain	21	0 - 63
Alps	-	------

* one sample
\+ unreliable, counted in wild habitats.

(4) Ciliation of floral parts: To record the observations arbitrary classes were devised after a preliminary survey had established the approximate limits of ciliation. The samples chosen for special comparison are 81 and 84 sent to the writer by Mr. Weatherby of the Gray Herbarium under the respective names of P. oliganthos R. & S., and P. juncoides Lam., var. decipiens (Barnéoud) Fern., and sample 89 collected by Dr. Hahn. These three samples come from the Atlantic American region where, as mentioned previously, differentiation has apparently taken place of a lax-spiked race of salt marshes (sample 81) and a dense-spiked maritime rock race (samples 84 and 89).

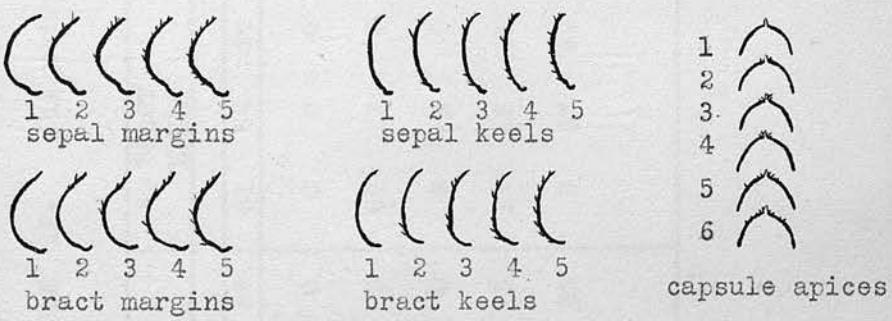


Fig. 1 Ciliation grades.

The two samples from maritime rocks differ considerably, which suggests that the expression of these characters is independent of the rock environment. The sepal keels of sample 81 are glabrous in contrast to the varying degree of ciliation observed for samples 84 and

TABLE IX. Ciliation of floral parts in per cent.

GRADE	BRACT MARGIN			BRACT KEEL			SEPAL MARGIN			SEPAL KEEL			CAPSULE APEX		
	SAMPLES														
	81	84	89	81	84	89	81	84	89	81	84	89	81	84	89
1	0	0	0	0	0	0	21	0	0	100	0	0	10	93	0
2	17	16	0	67	3	0	60	24	0	0	11	0	9	3	11
3	50	47	0	8	3	0	19	50	6	0	18	3	70	3	34
4	25	34	5	17	58	11	0	26	45	0	47	20	9	2	27
5	8	3	95	8	37	89	0	0	49	0	24	77	3	0	19
6													0	0	9

89, and there is evidence that the bract keels and sepal margins of 81 are also decidedly less ciliate. The position held by sample 81 with regard to the ciliation of the bract margins and capsule apices is not unique, Table IX.

An F_1 population (a plant of sample 56 (California) x a plant of sample 81) gave, for the five characters, percentages which fell midway between those recorded for sample 81 and those obtained for a population raised from selfed seed off the female parent.

No division can be drawn between the American and N. European samples. The averages of the grade percentages for America and N. Europe indicate that, for sepal margin and keel and capsule apex, the N. European population is the more ciliated, while for bract margin and keel the values are very similar. However, these average percentages have little or no regional significance because of the great intra-regional differences observed, e.g. the greatest and the least degree of ciliation of the bract margins was recorded from N. European samples.

(5) Number of seeds per capsule: Dowling (1936) dissected forty young capsules of P. maritima L. (British material) and of these thirty-nine showed three ovules. Her conclusion is that "in P. maritima there are usually only three ovules (p. 335) ----- usually two of these

ovules abort, giving a mature capsule with one seed" (p. 336).

In the samples from Europe two viable seeds per capsule is the typical maximum number, but in almost every sample examined occasional plants were found with a few capsules containing three or even four developed seeds. The N. American and Greenland samples, on the other hand, were found to have capsules with four developed seeds as the typical number, although most plants possessed a varying number of three-, two-, and less frequently one-seeded capsules. The number of seeds per capsule apparently affects to some extent the proportions of bracts and sepals. For instance a population bred from selected British parents was divided into two groups, (1) plants with 2-seeded capsules and (2) plants with 4-seeded capsules. The bract and sepal index values were then noted for each group with the following results:- bract index, group (1) mean, 1.86 ± 0.0263; group (2) 1.67 ± 0.0379: sepal index, group (1) 1.96 ± 0.0329; group (2) 1.85 ± 0.0313.

Crosses were made between plants from America with 4-seeded capsules and European plants with 2-seeded capsules. With the exception of the occasional occurrence of 3-seeded capsules on plants predominantly 2-seeded the

F_1 populations were 2-seeded. An F_2 population of 655 plants gave a ratio of 483 : 172 of plants with 2-seeded capsules : plants with more than two seeds. On the basis of a 3 : 1 ratio the observed figures agree closely with the expected 491 : 164.

(6) Self-fertility: The American and Greenland sea plantains have proved to be self-fertile in contrast to those of Europe which are self-sterile or are self-fertile only to a slight extent.

IV. THE ANALYSIS OF FERTILITY INTERRELATIONSHIPS OF SAMPLES.

Chromosome numbers: In 1934 McCullagh added to the previous list of Plantago chromosome numbers the counts for 22 species. A subsequent paper was to have included the results of a detailed cytological examination of the material grown at Corstorphine, but the programme was never completed owing to Miss McCullagh's death. She had, however, communicated verbally to the writer her counts for the Greenland sample and for some of the N. American and N. European samples. The work was then temporarily undertaken by Miss Bennett of this Institute. The material has now been handed over to Mr. Earnshaw of the Edinburgh and East of Scotland College of Agriculture and it is hoped that he will publish an account of his investigations in due course.

These workers have found that the material from N. America, Greenland and N. Europe has the diploid number 12, which is the number previously recorded for Plantago maritima L. Specimens from the Alpine samples 111, 112, 113, 113(a), 116 and 118 (see Table I) also have the diploid complement of 12, but in contrast the samples 62, 63, 65, 117 and 119 from the same region proved to be tetraploid with 2n = 24. The alpine region, unlike the others, therefore supports both a diploid and a tetraploid population.

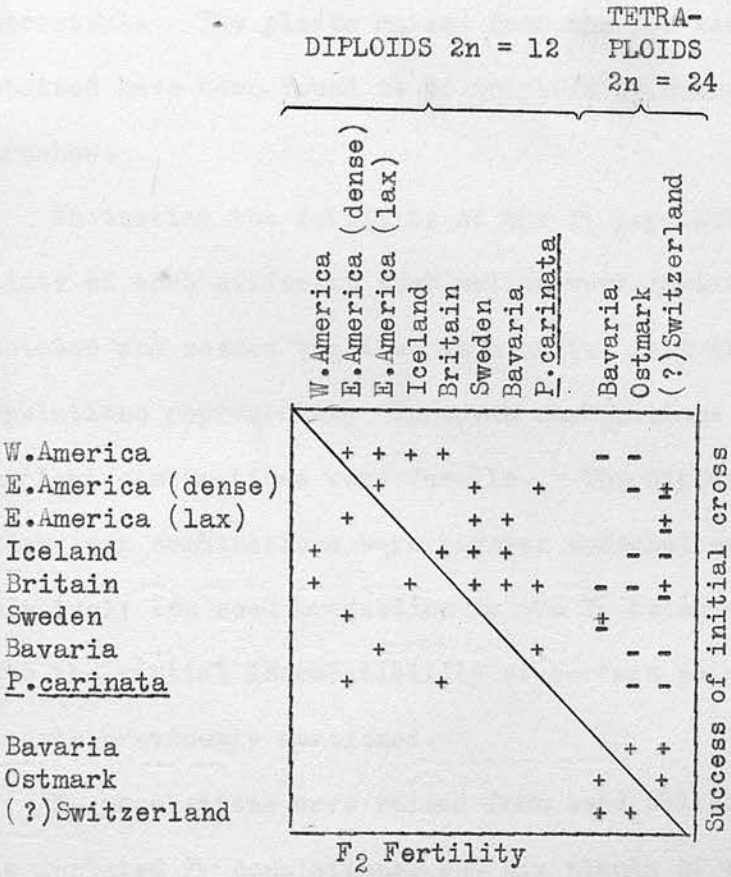
In taxonomic literature three species, P. maritima L., P. alpina L. and P. serpentina All. are recorded as inhabiting this Alpine region. The presence of P. maritima L. on the road-side between Mittenwald and Krünn in Bavaria, and P. serpentina All. near Scharnitz in Ostmark is reported in the literature: samples 62 from the former habitat and 65 from the latter have both been found to be tetraploid by McCullagh. According to McCullagh (1934) P. alpina L. is also tetraploid. Regarding this species Hegi (1906) states that it grows between 1300 m. and 2250 m. in Bavaria. Collections represented by samples 111, 112, 113 and 113(a) were accordingly made from this locality at elevations between 1200 m. and 1700 m. These samples have been found to be diploid by Bennett and

Earnshaw. Miss McCullagh had previously very kindly sent the writer her tetraploid specimen of P. alpina L. with a note to the effect that it had been obtained from the Royal Botanic Garden, Edinburgh. Enquiries at the Botanic Garden, however, revealed that its source is unknown, although the probability is that it had been obtained from Switzerland. Whether Miss McCullagh's specimen is a garden abnormality of P. alpina L. or whether it actually belongs to the Swiss tetraploid population as represented by sample 117 it is difficult to say. What is certain, however, is that in general the Bavarian and Swiss diploids correspond more closely to the accepted description of P. alpina L. than do the tetraploids from the same region.

Fertility relationships: In making the artificial hybridisations, self-incompatible female parents lacking the dominant leaf spot were, whenever possible, crossed with males carrying the dominant character, thus obviating the need for emasculation. Emasculation was only resorted to when self-compatible female parents were used or when the leaf spot character provided no check on the success of the cross. All crosses were made in cool greenhouses and the usual precautions relative to artificial pollinations were strictly observed.

The fertility results are presented in Table X. The success of the initial crossings, covering 34 out of a possible 55 combinations, is recorded in the triangle to the right of the table, while the fertility of some of the F_2 populations is given in the triangle to the left. In some cases where different parent plants were used to test the fertility of the same combination the crosses were not equally successful. Fertility irregularities were also observed in the F_1 populations. For instance the F_1 fertility of a cross W. America x Iceland was considerably lower than the fertility usually exhibited by wild-growing populations, although another F_1 population obtained by crossing the identical American specimen with another specimen from the same Icelandic sample proved to be fully fertile. Therefore when more than one pair of parents has been employed to test the interfertility of samples of two natural populations, the pair giving the highest seed yield has been taken as the standard of compatibility. When this standard approximates to the seed yield normally obtained for open-pollinated plants of a natural population a + sign has been entered in the table. It will be seen from table X that the diploid combinations, including P. carinata Schrad. (a diploid specimen of this species was obtained from Miss McCullagh),

TABLE X. Fertility interrelationships



\+ Fertile
± Partially fertile
\- Sterile

were mutually interfertile. The same is true for the tetraploid combinations. On the other hand when the diploids and tetraploids were intercrossed the results of the pollinations were either negative or only partly successful. The plants raised from the few seeds obtained have been found to be triploid by Bennett and Earnshaw.

In testing the fertility of the F_1 populations, six plants of each different combination were spatially isolated and seeded together as a unit. All the F_1 populations representing European combinations or American combinations were fertile. The diploid European x American combinations were however somewhat erratic, relatively low seed production in the F_1 being associated with the partial incompatibility of certain pairs of parents previously mentioned.

F_2 populations were raised from seed collected from the isolated F_1 populations, and six plants of each were similarly isolated. The results are recorded in the left triangle of Table X. It is worthy of note that the population of the combination Western America x Iceland, which in F_1 had had a decidedly sub-normal seed production, had by F_2 considerably increased its fertility.

V. THE SALIENT FEATURES OF THE ANALYSES.

1. The N. American, Greenlandic and N. European samples are diploid (n = 6). Those from the Alpine region are of two kinds (a) diploid, and (b) tetraploid (n = 12).

2. The N. American and N. European populations together with the Alpine diploids constitute one freely intra-fertile group while the Alpine tetraploids form another.

3. The N. American and Greenlandic plants are self-compatible and have capsules which are typically 4-seeded. In contrast the European plants are self-incompatible, or almost so, and have capsules which are typically 2-seeded. These characters exhibit the only abrupt transition which has been observed between the N. American and N. European populations.

4. The variate ranges for the measurable characters of all sub-regions overlap.

5. The bracts and sepals of the American samples are, on the average, relatively broader in proportion to length than those of N. Europe.

6. The sub-regional mean values of the bract and sepal indices and the ratio scape length : spike length follow a geographical gradient with low values in western N. America rising through eastern N. America, Iceland,

Faroes and Britain to maxima in Sweden and falling again in S. Germany.

7. The sub-regional values for the character leaf pubescence (see Table V) follow a geographical gradient, being relatively low in western N. America, rising in eastern N. America to a maximum in Iceland, thereafter falling steadily through Faroes and Britain, and reaching a minimum in S. Sweden, only to rise again in S. Germany.

8. The leaf-spot character which occurs commonly in samples from N. Europe, Greenland and eastern N. America has not been recorded in samples from the Pacific coast or from the Alpine region. The gene responsible for the expression of this character is therefore present in both continents but is not universally distributed in either. The sub-regional frequency percentages (Table VIII) form a semblance of a geographical gradient with low values in the Faroes and Britain and high values in northern N. Europe, Greenland and eastern N. America. Locally, however, the frequency values are peculiarly irregular.

9. In eastern N. America spike density follows an ecological gradient. The change from rock habitats to salt marsh habitats is accompanied by a change from

relatively dense spikes to relatively lax spikes. The presence of a dominant gene in this sub-region is apparently responsible for the expression of the lax-spike character. In Europe the exact equivalent of the lax gene is probably absent, which may account for the lack of such clear-cut differentiation into lax- and dense-spiked populations in this region. Nevertheless in Britain there is a tendency for the sea-shore samples to have slightly lower spike density values (12.54 flowers per cm.) than the inland samples (13.97 per cm.). This difference however seems to be at least partly due to the fact that the coastal samples have, on the average, longer spikes than the inland, a weak inverse correlation occurring between spike length and spike density (Davey & Lang, 1939).

10. Associated with the eastern N. American ecological gradient for spike density is a gradient for sepal index. The sepals of the rock samples are narrower in relation to their length than those of the salt marsh samples.

11. In Britain growth-habit and scape length follow an ecological gradient (Gregor, 1938). In the coastal areas growth-habit becomes progressively more erect and the scapes become progressively longer as the

habitat conditions change from water-logged mud to drained mud.

VI. CLASSIFICATION.

The units of orthodox taxonomy: The diploid sea plantains of Europe and N. America which have been treated in this paper are represented taxonomically by at least five species - Plantago maritima L., P. alpina L., P. carinata Schrad., P. juncoides Lam., and P. oliganthos R. & S. From the literature it would appear that P. maritima L. is the most widespread species, having been recorded from N. America as well as from Europe. But Fernald (1925) has drawn attention to the doubt in the minds of many American botanists as to the occurrence of this species in N. America. He concludes that N. America is represented by two species, P. juncoides Lam. (including P. decipiens Barnéoud and P. borealis Lange) and P. oliganthos R. & S. On page 93 Fernald writes "whether true P. maritima occurs in America is not wholly clear. In the Gray Herbarium there is a specimen typical in every detail marked Sitka (coll. Bongard) but all other Alaskan material seen is Pacific American P. juncoides Lam.".

The characters employed by Fernald to distinguish P. maritima of Europe from the Sea Plantains of N. America

are (1) higher bract and sepal indices, (2) greater ciliation of the sepals, (3) more slender capsules, (4) greater anther length and (5) a higher scape length : leaf length ratio.

Although no significant break in the range of sample mean values occurs for the bract and sepal indices between N. America and N. Europe, the indices are, on the average significantly lower in N. America than in Europe. But the broader sepals of N. American populations are not invariably less ciliate than the sepals of European populations with higher bract index values. In fact the sepal margins and keels of sample 89 from Atlantic America (bract index mean 1.86) were more ciliate than those of the British sample 21, the sample with the highest bract index mean value (2.25) in that sub-region. No correlations had been found between the bract or sepal indices and anther length (Davey & Lang, 1939). It is therefore not surprising to find that samples with the same anther length differ widely in respect of their bract and sepal indices. For instance sample 39 from Britain with an anther length of 1.80 mm., and sample 60 from Nova Scotia with the value 1.79 mm., have respectively sepal indices of 2.33 and 1.61. And finally, while a high scape length : leaf length ratio is reputed to be diagnostic

of P. maritima of Europe, the ratio of 1.18 for the British sample 35 is lower than any recorded for the Atlantic American samples.

Fernald (p. 95) states that "In the northern half of its range P. decipiens becomes very dwarfed, with scapes only 1 - 7 cm. long and spikes 0.5 - 2 cm. long. This is the plant of Greenland, Iceland and Arctic Europe described and beautifully illustrated by Lange". According to Ostenfeld & Grøntved (1934) P. maritima also occurs in Iceland, and therefore a critical examination of the Icelandic samples became necessary. If both these authors are correct then the ranges of P. juncoides Lam. and P. maritima L. are coincident in this area, a circumstance which might account for the lack of discontinuity in respect of the bract and sepal indices between the N. American and N. European populations. But an examination of the character mean values and more particularly of the variate ranges of the seventeen samples from Iceland gives no support to the contention that Iceland is inhabited by two distinctive populations; neither is this Icelandic population distinct from those of the Faroes and of Britain. If a specific distinction between the N. American and N. European populations were to be made at all it would be more appropriate to draw

the line between Greenland and Iceland than to postulate the existence of a N. American species in Iceland, for it is between these two countries that the only marked character changes occur, viz. the changes from 4-seeded to 2-seeded capsules, and from self-compatibility to self-incompatibility.

Samples 84 and 81 represent respectively P. juncoides Lam. and the eastern American species P. oliganthos R. & S., and as they were collected by Mr. Weatherby of the Gray Herbarium they can be regarded as authentic samples. The characters attributed to the species P. juncoides and P. oliganthos have been found to vary quantitatively and, while a minority of variates in a sample may exhibit characters conforming to the specific type, the majority have characters which can be found in some proportion in all samples. In the case of samples 84 and 81 only a relatively small number of the variates possessed by the latter have characters peculiar to that sample. For instance, of the total constituents of sample 81, 21% were found to have sepal margins less ciliolate than the least ciliolate variates of 84, 10% had capsule apices less ciliolate, 10% had larger seeds, 9% had a lower scape length : leaf length ratio, and 7% had spikes more lax than the least densely spiked variates of 84. None had

bract margins and keels less ciliolate, nor did any have thicker leaves than variates in 84. These characters are diagnostic of the two species, but as the above treatment shows,the difference between 81 and 84 is far less dependent on character combinations peculiar to one or the other than on differential frequencies of individual characters common to both samples. An estimate of the extent by which populations differ from each other can be obtained by employing the aggregate difference method described and used by Anderson & Abbe (1934, p. 47). Provided the same characters, measured on the same scale, are utilised in making comparisons the aggregate difference gives an indication of the magnitude of population divergence. For comparative purposes the two samples 81 and 84 have again been used, together with sample 89. This latter sample is also from eastern America and in appearance resembled 84 more than it did 81, a general observation which is given more precise expression below. In respect of the mean values for the characters of the spikes, bracts, sepals, seeds, anthers, capsules and leaves (22 characters in all) the aggregate difference between samples 81 and 84 has been found to be 4.45; between 84 and 89 the index is 4.18; while between 81 and 89 it is 6.84. As far as the individual characters which

contribute to those indices are concerned sample 84 also occupies an approximately intermediate position between 81 and 89. Thus while both 84 and 89 differ quantitatively from 81 by a group of characters, the greatest divergence is exhibited by 89. It might therefore be considered that herein lies the distinction between P. oliganthos, as represented by 81, and P. juncoides. But this is not the case since many of the characters distinguishing 81 from 84 and 89 are not the ones distinguishing 81 from P. juncoides in other parts of its range. For example if the individual mean values for the measurable characters of spikes, bracts, etc. of sample 81 are taken as unity, and if the mean values for the same characters of samples 84, 89 and a western American sample 86 are given their proportionate value above or below this standard, it will be seen (fig.2) that, in the aggregate, the difference between 81 and 89 is actually less than the difference between 89 and 86, a sample from an area where P. juncoides alone grows. In fact it would not be difficult to find individual specimens outside the eastern American sub-region which could with some justification be referred to P. oliganthos R. & S. Similarly some of the rare plants with 4-seeded capsules which occur in widely separated European localities might easily be

Fig. 2 The relative position of sample 81.

confused with P. juncoides Lam.

Too great a reliance on specific descriptions may lead to the recording of distributional anomalies. For example Whyte (1869) has recorded the presence of three species P. maritima L., P. alpina L., and P. serpentina Vill. from the Scottish mountains, while Hegi (1906) records the occurrence, though as uncertain, of P. alpina in Iceland. There is no doubt that a few plants conforming to the description of P. alpina are to be found not only in Britain and Iceland but also in the Faroes. However, there seems to be no reason for assuming that such exceptional variates represent a population within a population. More pertinent are speculations as to whether P. maritima occurs in the alpine region, because in this region there occur tetraploid populations containing many variates which cannot be distinguished morphologically from diploid variates belonging to British and Swedish samples, e.g. the tetraploid population (sample 62) on the road-side between Mittenwald and Krünn in Bavaria.

The units of experimental taxonomy: A disadvantage of the present system of classification as far as the experimentalist is concerned is that the taxonomic units do not always coincide with the categories of variation.

The Mittenwald population is a case in point. Unfortunately this objection is inherent in a system in which the units are founded on a complex of attributes irrespective of their individual variational significance. If, instead, the attributes of populations were to receive individual treatment it would then be possible to record by means of the same notation both the variational type and the taxonomic status of populations exhibiting these separate attributes. The potential ability of members of a population freely to exchange genes would seem to be a fundamental "specific" criterion of variational significance. From the result of hybridisation experiments it has been seen (Table X) that, when given an opportunity to hybridise, the N. American - N. European - diploid Alpine population (comprising P. juncoides Lam. (including P. decipiens Barnéoud and P. borealis Lange), P. oliganthos R. & S., P. maritima L., P. alpina L., and probably P. carinata Schrad.) constitutes a single intrafertile group, although in such a widespread population the potential gene exchange is not realised in nature owing to the spatial isolation of its parts. But as the adoption of the criterion of gene exchange would involve a redefinition of the taxonomic term species it is proposed to avoid this term in a complementary system of classification and to employ

in preference the term Coenospecies (Turesson, 1922) for a group of sexually reproducing plants separated from other groups by sterility or by the failure of the hybrid to produce viable seeds. The coenospecies is then "that stage of evolutionary divergence at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding" (Dobzhansky, 1935, p. 354). A coenospecies is more likely to represent a Linnean species or group of Linnean species than a population within such a species, but whatever the range of morphological variation the criterion would be its inability to exchange genes with other populations, even when given the opportunity of so doing. All parts of the diploid Sea Plantain population belonging to the P. maritima group would therefore belong to the same coenospecies, i.e. to the same category of variation. The inclusion of the alpine tetraploids in this coenospecies must await proof of gene exchange between them and the diploids. Proof that these tetraploids and diploids can be crossed has already been obtained.

"Species arrange themselves in natural groups because some of them have a slight (low) capacity for exchanging genes" (Clausen, 1936, p. 522). Units of this order

within a coenospecies have been termed ecospecies (Turesson, 1922), one ecospecies being separated from another by restricted interfertility and by failure of hybrids to establish themselves in nature. Clausen (p. 522) believes that "ecospecies should be regarded as the taxonomic species, because they represent the smallest units which keep separate by the aid of an inner balance mechanism". The maintenance of their individuality he regards as being due to the destruction of hybrids under natural conditions "and the few vigorous offspring left will largely drop back into one or other of the two original species, sometimes adding one or a few genes from the other, thus increasing their variability and creating the phenomenon of parallel variation as described by N. J. Vavilov".

Since no inherent restriction is imposed on the free exchange of genes between parts of the diploid plantain population and since no lack of vigour has been observed in the F_2 generations, all the diploids belong to the same ecospecies. If it should be found that the diploid and tetraploid groups are capable of exchanging genes, then they would belong to different ecospecies of the same coenospecies (see p. 51 eco-maritima), if not, the two groups would belong to separate coenospecies.

Now when dealing with morphologically differentiated populations, which are physiologically capable of freely interbreeding, i.e. populations within an ecospecies, it is necessary to consider their permanency as distinctive morphological units. To describe a population in terms of a peculiar combination of characters and allocate populations to different categories on the basis of the observed degrees of difference between combinations implies that for taxonomic purposes such combinations bear a static relationship to one another. But all evidence favours the view that few populations, especially the smaller breeding communities,are morphologically stable, even temporarily. The gene complexes of small Sea Plantain communities are ever susceptible to change resulting from the periodic attacks of grazing animals, the partial or complete depopulation of existing habitats by flood action, and the repopulation of old and the colonisation of new habitats. Even the larger communities are not immune to the effects of environmental fluctuations such as climatic variations. Elton's (1924) work on the fluctuations in animal numbers suggests that short-period pulsations of climate operating over wide areas affect the genotypes of large populations in as much as "every time a minimum in numbers occurs, there is a chance of the less common genes becoming extinct" (p. 159). On

On the other hand when recolonisation is in progress the chance of any individual surviving is greatly increased. It follows, therefore, that an inventory, if that were possible, of every morphologically discrete population, i.e. one possessing its own peculiar range of morphological variation, would be no sooner completed than it would be out of date.

It would, nevertheless, be a mistake on the part of taxonomists to ignore altogether minor populations, e.g. breeding communities, on account of their instability, because they just as surely represent links in an evolutionary network as do the more obvious units of higher taxonomic rank. But the problem of recording population differentiation is further complicated by the fact that when spatial isolation is less than absolute, breeding populations must to some extent interbreed with their neighbours, and thus gene exchange between breeding communities has also to be considered. If, therefore, instead of attempting to describe a multitude of populations in terms of their discontinuities in character complexes, taxonomic emphasis were to be transferred to recording the populations typifying particular kinds of variation, e.g. geographic, ecologic etc., regardless of the actual degree of aggregate morphological distinctness exhibited

by individual populations, then the simpler problem of studying individual "indicator" characters (in contrast to complexes of characters) would be involved. That is, from the taxonomic standpoint, inherent morphological and physiological attributes of populations would be used mainly as indicators of the natural arrangement of populations in response to factors external to the plants themselves. In this way the discontinuities, proportional representations and trends in the distribution of individual characters and their variations could be assessed in terms of populations having either discrete or overlapping distributions. For example, the leaf spot character previously mentioned is an "indicator" carried by a geographical population covering northern Europe and eastern America; its local absence within this area is indicative of a chance fractionation of a population followed by spatial isolation. The European portion of this leaf spot population lies within a 2-seeded capsule population, while the American part lies within a 4-seeded capsule population. Within Britain the three growth-habit categories, decumbent, ascending and erect, have been used (Gregor, 1938) as indicators of the ecological relationships of populations.

A form of differentiation within the ecospecies is when a character's expression tends to change quantitatively and progressively from one place to another. The variations of the characters bract index, sepal index, scape length : spike length ratio, and leaf pubescence exhibit this particular kind of geographical relationship in as much as when their sub-regional mean values are treated in geographical sequence the variation in character expression follows a geographical gradient. These gradients, however, are not coincident, the characters varying independently of each other in different geographical directions. This is shown in fig 3, where the bract index, sepal index, scape length : spike length ratio, and leaf pubescence gradients are represented graphically by connecting the sub-regional character mean values. The vertical lines represent the sub-regional variate ranges while the small horizontal lines mark the extremes of the range of the sample mean values. In the case of the leaf-spot character, local differences in the frequency of spotted plants, differences which are apparently due to chance, are very pronounced and make it impossible to demonstrate even a semblance of a geographical gradient within sub-regions. But the average sub-regional percentage frequencies do tend to

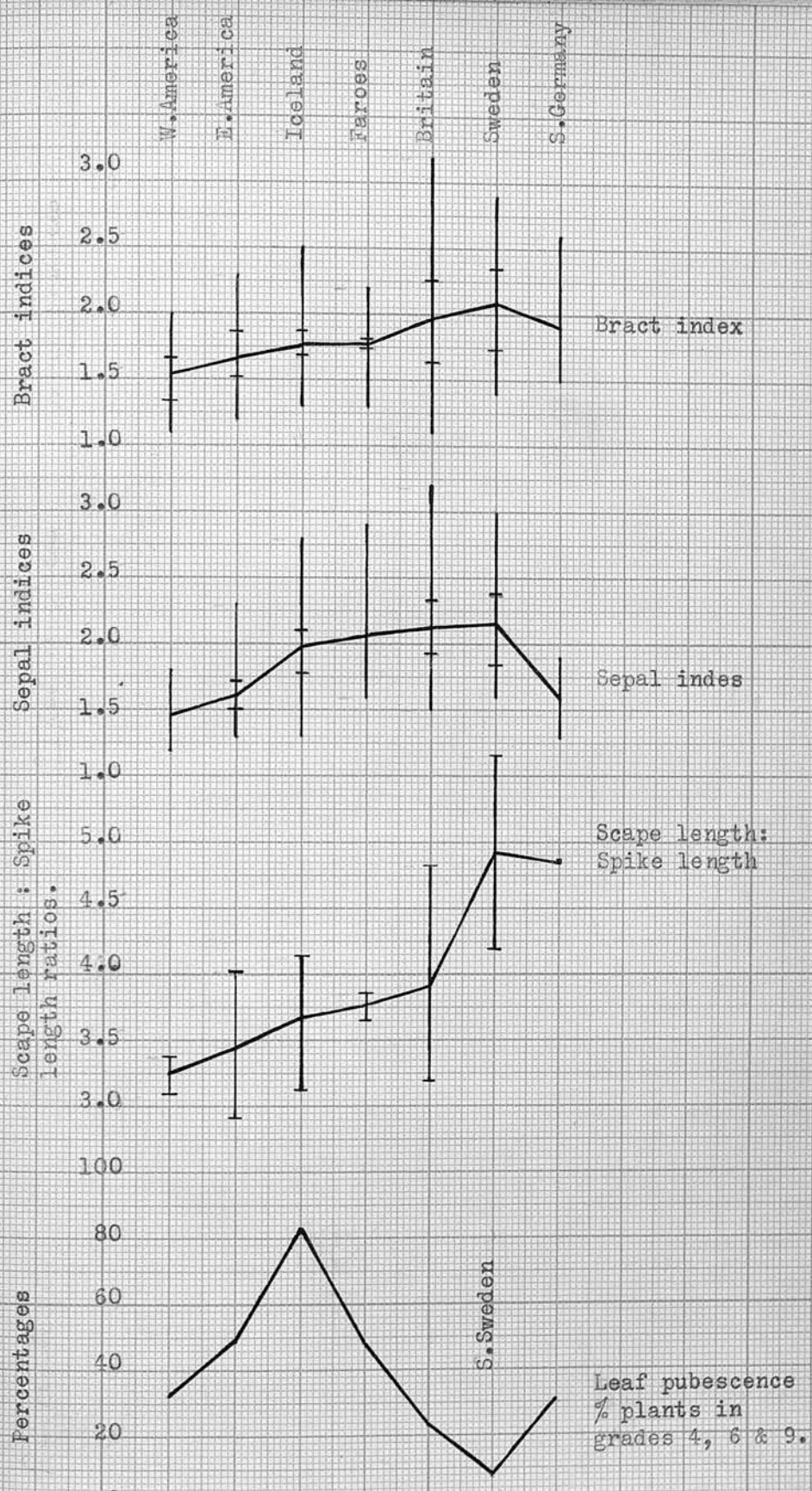


Fig. 3. Bract index, scape length : spike length and leaf pubescence. GEOCLINES.

Fig. 4. Leaf spot GEOCLINE.

follow a geographical sequence (fig. 4).

Another kind of gradient in character expression which, unlike the above, does not necessarily follow a geographical sequence is exemplified by the characters growth-habit and spike density. In Britain the change from water-logged to drained coastal habitats is accompanied by an increase in scape length and a more erect growth-habit (see Gregor, 1938). No geographical gradient in respect of these characters has been established for Britain, nor was it likely that such a gradient would be found owing to the irregular distribution of the different kinds of habitat. Locally, the environmental change from one habitat to another may be considerable and abrupt, but taking the British sub-region as a whole the variation between the one extreme and the other is continuous. Corresponding to the habitat-continuity, a continuous range in sample mean values has been found for scape length and growth-habit (fig. 5). In much the same way spike density in eastern America follows an ecological gradient from salt marsh to maritime rock habitats (fig. 6).

Variation which follows either a geographical or ecological gradient may be said to be clinal, and populations possessing characters which behave in this manner can be recorded under the taxonomic title cline

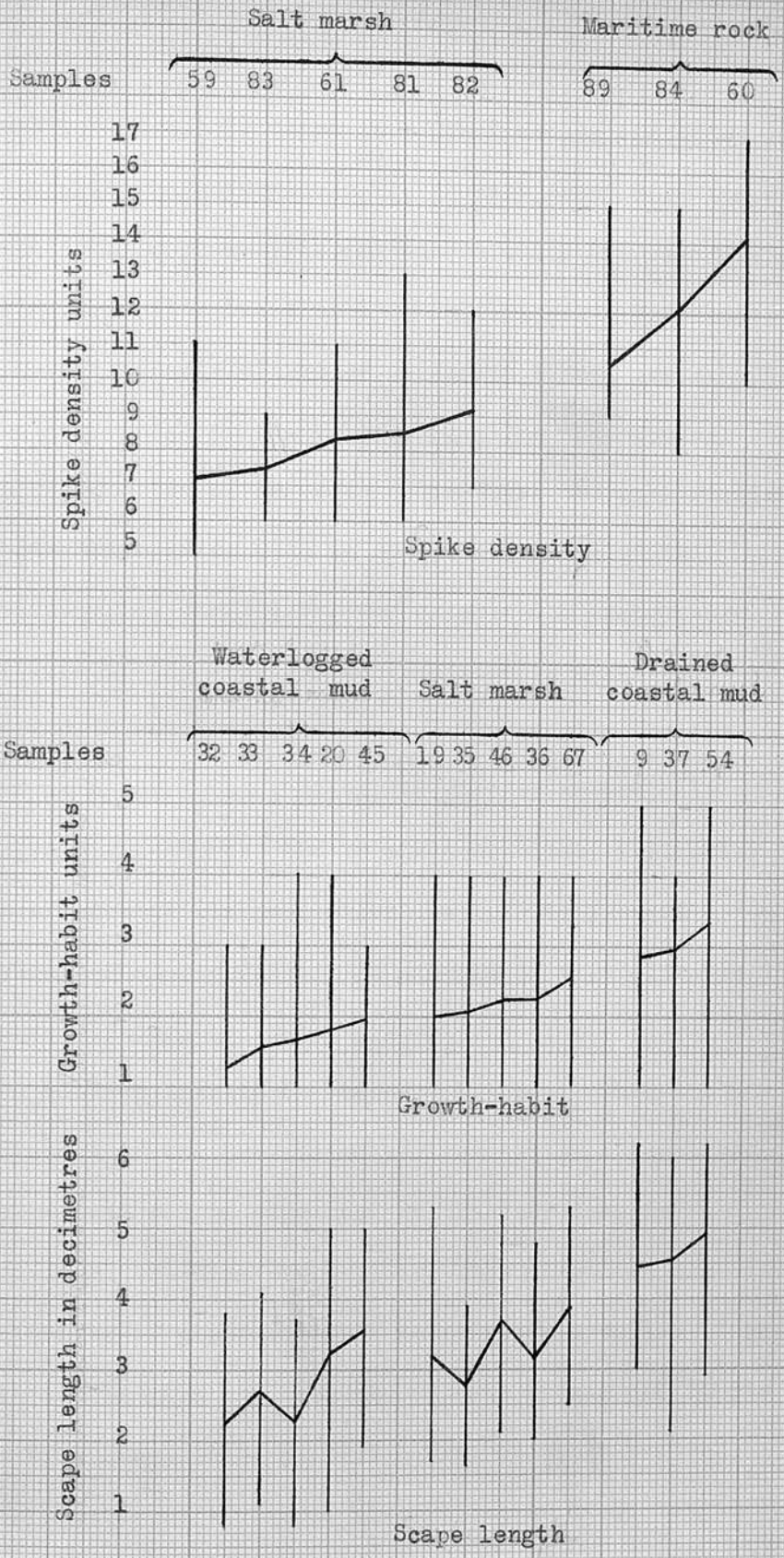


Fig. 5. Spike density & growth-habit ECOCLINES.

(Huxley, 1938). A cline is defined as any gradation in measurable characters. In the present paper only those gradations in phenotypic characters which are regarded as having a genetic basis will be considered. Prefixes can be used to denote clines of different types, for example geocline (geographical cline), ecocline (ecological cline). The recognition of an ecocline involves the appreciation of its correlation with an observable gradient in environmental conditions, for example the scape length ecocline of the British Sea Plantains is apparently adapted to edaphic variations. The geocline on the other hand is a character gradient tracing an essentially geographical course, but in all probability reflecting the effects of its past as well as of its present environmental contacts. An example of a geocline is the progressive change in the proportions of the floral bracts from western America to northern Europe. That the influence of the prevailing environment on a geocline may be indirect is suggested by the fact that, in individual breeding communities, scape length (a character indicative of plant size) is correlated in var~~ious~~ying degrees with the lengths and breadths of both bracts and sepals (Davey & Lang, 1939, p. 19). The, at least partial, interdependence of floral proportions on scape length is

further demonstrated by the sample mean values in respect of scape length being correlated with the bract index and sepal index means, the respective values of r being +0.64 and +0.32. However, the regression coefficients show that bract index rises by 0.014 and the sepal index by only 0.007 for every increase of 1 cm. in scape length. Therefore in terms of index values the general effect of scape length on bract and sepal proportions, significant only in the case of bracts, is not sufficiently pronounced to obscure the local operation of contributory factors such as differences in the number of seeds per capsule and the differences in spike density; the latter character is sometimes correlated with the bract and sepal dimensions, independently of scape length (Davey & Lang, 1939, p. 7). It follows then that the bract and sepal index geoclines, while exhibiting no apparent coincidence with perceptible environmental gradients over their whole distributions, must in any given locality be seldom, if ever, entirely free of the influence of the prevailing environment acting indirectly through the medium of associated characters.

Treatment by clines thus provides a method of recording separately the various geographical and ecological trends in character expression, while a collective examination of clines makes it possible to

trace the local relationships of character combinations. For example the combination low sepal index - low spike density is a characteristic of the salt marsh samples of eastern America, but the same sepal index is, in other parts of the American Continent, associated with a relatively high spike density, e.g. in Alaska (sample 86).

As previously mentioned, however, abrupt character changes which follow no clinal sequence occur and differentiate parts of a large population. Such differentiation may be due to the presence or absence of one component of a contrasting character pair. For instance the eastern American-northern European population possesses a leaf-spotting gene which is apparently absent from Pacific America and the Alpine region. Differentiation of this abrupt kind may be said to be extraclinal. On the other hand it may be necessary to refer to particular ranges (distributions) on a geocline, e.g. to the Icelandic range of the leaf pubescence cline or to the N. American range of the sepal index cline, etc. Such population differences are intraclinal. It is proposed to apply the term geotype to both extra- and intraclinal geographical variation and to define a geotype as follows:
a population in a geographical region possessing characters differing from those of another region. A geotype may be

extraclinal if it does not fall within a geographical gradient in phenotypic characters, or intraclinal when it refers to a particular range within a geographical character gradient. The term geotype has already been used by Remane (1928, pp. 65 and 75) to denote a geographical race and therefore the term as defined above is an elaboration of his definition.

It will also sometimes be necessary to make reference to populations within an ecocline. Populations which occupy particular ranges on an ecocline are ecotypes (Turesson, 1922), e.g. the British populations exhibiting a predominating frequency of ascending variates belong to the "ascending" ecotype of the "growth-habit" cline. It should perhaps be emphasised that the categories of geotype and ecotype are population concepts, not morphological classes. That is to say, a decumbent individual from a population classified as an ascending ecotype would, despite the fact of its being decumbent belong to the ascending ecotype, and not to a taxonomic category comprising only decumbent variates.

A considerable amount of local differentiation may occur between isolated populations due primarily to the chance fixation of characters of no ecological significance or, at most, of wide environmental tolerance.

For example in Britain (i.e. within the distribution area of the leaf spot geotype) isolated populations lacking the leaf spot gene are to be found. Such differentiation is probably partly due to predetermined variation and partly to subsequent random variations in the gene frequencies (see Wright, 1932, and Dobzhansky, 1937, p. 134 et seq.). Populations locally differentiated, but lacking apparent adaptive significance, could be referred to as geoecotypes (Gregor, 1931) which are defined as locally differentiated populations which may occupy similar habitats, and which are considered to have arisen by the chance fractionation of a parent population. A geoecotype, then, is in a sense a micro-geographical population whose individuality is recorded in terms of an indicator character which, though tolerant of the prevailing environment, is not perceptibly correlated with any particular kind of habitat.

The above terms have reference only to population characteristics but it not infrequently happens that striking variates, e.g. golden chlorophyll-deficient plants, plants with leaf-like bracts etc. occur so rarely and so sporadically that they never become a feature of any population or group of populations. For genetic, economic or other reasons it may sometimes be necessary

to record the occurrence of these exceptional hereditary aberrations, and the term exotype (Remane, 1928) would seem to be an appropriate one to use in this connection.

The application of reference names: The accepted bi- and trinomial nomenclature would apply to the respective "species" units - the coenospecies and ecospecies. But populations accredited to the various geographical and ecological categories would require nothing more than descriptive symbols, and in most cases the name of the distinguishing character, or some suitable abbreviation, would be sufficient designation. For example the description "immaculate" might conveniently be given to the geotype lacking the leaf spot gene; this abbreviation would of course also apply to the geoecotype which lacks the same gene. These populations under their respective categories could then be presented in list form below their appropriate coenospecies or ecospecies. By this arrangement the spatial associations of characters, e.g. of geotypic and ecotypic characters, could be assessed at a glance. Any attempt to apply an extension of the trinomial system to such populations would not only be confusing but misplaced, as it might suggest a progressive subordination of categories which has never been implied. A classification of the diploid

Sea Plantains of N. America and Europe based on the available data and incorporating the foregoing suggestions can be summarised as follows:-

COENOSPECIES: Plantago coeno-maritima including the diploid populations of P. maritima L., P. alpina L., (?) P. carinata Schrad., P. juncoides Lam., P. decipiens Barneoud, P. borealis Lange, and P. oliganthos R. & S.

ECOSPECIES: P. coeno-maritima eco-maritima (see p. 39)

GEOTYPES (Extraclinal):

(a) Self-compatible, capsules typically 4-seeded.
N. America and Greenland.

(b) Self-incompatible, capsules typically 2-seeded.
Europe.

(c) Leaf Spot presence ("maculate")
N. Europe, Greenland and eastern N. America.

(d) Leaf Spot absence ("immaculate")
Western N. America and Alps.

CLINES:

(a) Bract Index, geocline (see fig. 3).
GEOTYPES (intraclinal): (1) N. American, mean = 1.61, range of sample means = 1.33 - 1.86; (2) N. European, 1.93, 1.62 - 2.35.

(b) Sepal Index, geocline (see fig. 3).

GEOTYPES (intraclinal): (1) N. American, 1.58, 1.45 - 1.71; (2) N. European, 1.93, 1.78 - 2.38 .

(c) Scape length : spike length ratio, geocline (see fig. 3).

(d) Leaf pubescence, geocline (see fig. 3).

(e) Leaf spot, geocline (see fig. 4).

GEOECOTYPES: (1) "maculate" (100% spotted), (2) "immaculate" (0% spotted).

(f) Spike density, ecocline (see fig. 5).

(g) Growth-habit, ecocline (see fig. 5).

ECOTYPES: (1) "decumbent", (2) "ascending", (3) "erect".

EXOTYPES:

(a) "Golden" (a chlorophyll deficient).

VII. SUMMARY.

1. It is suggested that experimental taxonomists should in the meantime refrain from attempting to meet their requirements by redefining the orthodox classificatory categories, but should, instead, use a complementary system of classification with a distinctive terminology.

2. It is also suggested that taxonomic emphasis might be usefully transferred from morphological character complexes to individual morphological and physiological attributes indicative of particular kinds of differentiation.

3. The use of the following "specific" terms is advocated -

Coenospecies, a population which is incapable of exchanging genes with other populations, even when given the opportunity.

Ecospecies, a population with an inherently low capacity for exchanging genes with other populations of the coenospecies.

4. The use of the following "infra specific" terms is advocated for populations actually or potentially capable of freely exchanging genes -

Cline, any gradation in measurable characters.

Geocline, a cline following a geographical gradient.

Ecocline, a cline apparently correlated with an observable ecological gradient.

Geotype, a population in a geographical region possessing characters differing from those of another region. A geotype may be extraclinal if it does not fall within a geographical gradient in character expression, or intraclinal if it has reference to a particular range on a geographical gradient.

Ecotype, a particular range on an ecocline.

Geoecotype, a micro-geographical population primarily the result of a chance fractionation of a parent population.

Exotype, an hereditary aberration which occurs so rarely and so sporadically that it never becomes a feature of any population: the category of exotype is therefore not a population concept.

I am much indebted to those biologists whose names appear in Table I for their generous help in collecting material, and to Mr. J. S. L. Gilmour and Dr. Julian Huxley for valuable suggestions and criticism.

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THE ECOTYPE CONCEPT IN RELATION TO THE REGISTRATION OF CROP PLANTS

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CONTENTS.

Introduction.

The genetic study of the mutual relationships between plant populations and their habitats, to which the term *Genecology* has been applied by Turesson (1922), is a step towards the recognition of the smaller taxonomic units as they are realised under natural conditions. Genecological research has revealed the fact that, in nature, species-populations may contain groups of plants which, apparently by reason of the influence (primarily selective) of the prevailing environment, have come to possess a certain genotypic constitution suited to the conditions of life in their particular habitats. These aggregations of genotypes compatible with a particular habitat have been termed *ecotypes* by Turesson (1922), and their measurable characteristics are capable of numerical expression in terms of the mean or modal values of their predominant morphological and physiological features. The ecotype constitutes the smallest unit in

a new system of classification proposed by Turesson, and may be regarded as a product arising from environmental fractionation of larger genotype complexes called *ecospecies*. This latter term denotes the genotype compounds as they are present in nature, but, since these units have somewhat circumscribed capabilities which limit the possible occurrence of certain combinations under natural conditions, the term *coenospecies* has been given to designate the total sum of possible combinations in a genotype compound (Turesson, 1929).

I. The ecotype concept.

The nature of ecotypes.

The ecotype concept postulates that the ecotype unit be regarded as the result of the sorting and controlling effect of the habitat factors (*e.g.* climatic, edaphic, and biotic) upon the various genotypes within a species-population. While there is evidence that external environment can cause the origin of new genotypes, a habitat is not considered to be a directive agent responsible for the origin of genotypes specially adapted to the prevailing conditions, but, in general, as far as the genotype is concerned, is held merely to act as a passive agent, supplying an adequate environment to a population of a suitable genotypic constitution. The ecotype is, therefore, a genotypically complex unit whose constituents are capable of resisting elimination under the prevailing habitat conditions; its survival in a particular habitat is not necessarily dependent on the morphological characters phenotypically displayed, but rather on the maintenance of a state of harmony between its genotypic components and the habitat. There are, however, instances of an intimate relationship between certain definite environmental conditions and a particular habitus; in such cases the latter is sometimes the phenotypic exhibition of a special *reaction type*, which is developed by certain genotypes and is essential for their survival, *e.g.* dwarf growth in exposed situations (Turesson, 1922; Gregor and Sansome, 1927; Gregor, 1930).

Although experimental evidence indicates that an ecotype is the result of the continuous elimination of unsuitable genotypes by the environment, yet the constituent genotypes are, within limits, capable of fluctuant change as a result of the direct effect of external conditions. This modificatory capacity of individual genotypes and collective genotype groups permits within a population a range of expressional adjustment to take place in response to fluctuating environmental conditions,

and must contribute considerably to the success of such units in nature[1]. While minor modifications are of frequent occurrence, it would seem that, in general, the controlling influence exerted by change of environment expresses itself more in an alteration of the proportions in which the genotypic constituents of a population occur than in a direct modificatory effect on the population as a whole. If this were not the case, the parallelism which has been demonstrated experimentally to exist between the habitats and the genotypic constitution of their populations would be much less commonly realised. It has also been observed, *e.g.* in *Succisa pratensis* Moench (Turesson, 1922) and in *Plantago maritima* L. (Gregor, 1930), that the modificatory influence of the environment may operate in a direction parallel to that of genotypic selection, *e.g.* when a population composed of hereditary dwarf variations is further reduced in height by the direct influence of its habitat conditions. Moreover, in extreme habitats, modifications may mask the normal genotypic expression to such an extent that a population, in reality composed of different genotypes, may appear to be phenotypically homogeneous. There are cases in which the degree of expressional adjustment of a genotype complex has been so pronounced that a single ecotype within one species-population has survived in two different habitats, *e.g. Lysimachia vulgaris* L., while in another species-population the same two kinds of habitats have been occupied by distinct ecotypes, *e.g. Lysimachia nummularia* L. (Turesson, 1922, p. 216).

Ecotypic adaptability.

The presence of monogenotypic ecotypes in allogamous species-populations must indeed be of rare occurrence, and consequently it should not be assumed that a population must inevitably suffer extinction when the balance between its environment and genetic constitution is disturbed. Provided that the environmental change does not result in the death of all the various genotypes, it is conceivable that a readjustment of the constituent parts will take place, until once more a state of equilibrium is attained. It is, however, to be expected that the ecotypes represented at the limits of environmental distribution will be more specialised than those occupying the central area where optimal conditions prevail. Thus the specialisation of the inhabiting forms will become more pronounced as the conditions become more extreme. The populations occupying extreme

[1] The modifications in the phenotypic expression of genotypes following environmental changes are being studied by the Division of Plant Biology, Carnegie Institution, in U.S.A. (Hall, 1932), and by the British Ecological Society in England (Marsden-Jones and Turrill, 1930).

habitats may therefore be assumed to comprise a reduced number of genotypes, and, since the power of an immobile ecotype to resist changed circumstances must depend largely on the number of its component genotypes, these highly specialised ecotypes will possess a low potential adaptability, and will, in consequence, be more liable to extermination than more richly endowed populations. Ecotypical adaptability therefore is dependent on genotypical heterogeneity.

The dispersal of ecotypes.

There is evidence that similar, though separated, habitats are frequently occupied by habitat-types which bear such a striking resemblance to each other that they may be considered as belonging to the same ecotype. This re-appearance of a particular ecotype under like environmental conditions is well illustrated by the fact that, wherever the *Hieracium umbellatum* population on the Swedish west coast has been investigated, the sea-cliff localities have been found to harbour only the broad-leaved, sea-cliff type. The beach dune localities which alternate with the cliffs have, conversely, been found to support only the dune type (Turesson, 1922, p. 337). There is a marked similarity between the populations occupying the different sea-cliffs and also between those inhabiting the various dunes within their comparatively limited area. This resemblance is probably due to the genotypes having migrated from some region in close proximity to their present habitats. On the other hand, it may happen that the invasion of similar habitats is accomplished by populations of a species-population only after these have experienced a long period of migration from their optimal centre, or centres, of dispersal across dissimilar intermediate ecological regions. In such cases the ultimate habitat populations might exhibit recognisable morphological differences as resulting from a differential elimination of genotypes during the passage of the various migrant streams.

The occurrence of spatially isolated populations (geo-ecotypes).

The establishment of ecotypes in nature presumes that impediments to free sexual reproduction, within the bounds of a species-population, are imposed by environmental conditions, and that strict spatial separation is not a necessary accompaniment of ecotypic differentiation (Gregor, 1930). On the other hand, the erection of an insurmountable barrier in the territory occupied by a genotype complex, or the transportation of a part of a genotype complex by chance agencies from one habitat, across existing obstacles to another environmentally tolerable habitat, would occasion the complete spatial isolation of the population. Therefore,

just as an ecotype is a distinct part, preserved by ecological isolation, of a larger population, so these genotypes, separated as a result of a chance circumstance, might constitute distinctive units preserved by geographical (spatial) isolation.

Numerous instances are known of the occurrence of spatially isolated, but environmentally similar, habitats harbouring different forms of the same species-population. This, however, should not for various reasons be employed as an argument against the environmental control of genotype distribution, because, firstly, a population must be more or less in tune with the environment before it can become established in any new habitat. Secondly, there is no proof that isolated populations, *e.g.* the Hawaiian snail populations which inhabit different valleys on the island of Oahu (Gulick, 1905), are not merely chance introductions of certain genotypes from an ecotype already established in a similar habitat elsewhere. Thirdly, although two habitats may originally have been populated by like genotype complexes, subsequent temporary differences in environment may have brought about a differential elimination of genes, thus leading to the occupation, by dissimilar populations, of what are now similar habitats. The actual existence of geographically isolated intra-ecotype groups, which differ morphologically from each other, has been demonstrated by Turesson (1927) within the lowland ecotype *Poa alpina pediaca*.

It would seem probable, therefore, that many of the differing populations, which are taxonomically recognisable and occur in similar, though separated, habitats, may represent parts of an ecotype, while their respective differences in character are due to a limited genotypic representation of the parent populations at the time of separation. Such differences would be maintained and accentuated as a result of spatial isolation. The term *geo-ecotype* has been proposed (Gregor, 1931) to include these units so intimately connected with the ecotype, whose characteristics, however, are dependent on geographical (spatial) isolation following their chance introduction.

Uniformity of the ecotypic units.

It has been shown that the various genotypes of a species-population, occupying an environmentally subdivided region, do not become established indiscriminately throughout the entire area, but that a grouping of suitable genotypes into more or less physiologically isolated ecotypes, takes place in accordance with the differences in habitat conditions. Individual ecotypes, therefore, do not represent the total genotype complex of the unit to which they belong. This fractionation may

either take place by the chance introduction of a few homozygous or heterozygous plants into a new habitat, or by the prohibition of certain genotypes and the entrance of others during the process of normal migration. Nevertheless, once a collection of plants has invaded a habitat, the elimination of genes within the colony may still continue; some genotypes may be immediately suppressed, some may be capable of vegetative development but fail to produce seed, others may, in this respect, be more able to cope with the habitat conditions, while still others may ripen abundant seed. It is unlikely that more than a small proportion of the seeds produced annually will reach the reproductive stage; it is, however, probable that those individuals which are capable of producing the most seed will stand the greatest chance of leaving progeny. According to Hagedoorn (1921, p. 120): "Wherever the group is continued from a fraction of the number of individuals, or where a colony is started by a few individuals, the chance of the heterozygotes to be included in the group or to have heterozygous children included, is proportionate to their frequency. Heterozygotes will produce homozygotes but not the reverse." Further, in "every case in which rare individuals having genes, not present in the majority, or in which rare individuals being impure for, or lacking in genes, common property of the majority, happen to be excluded from the number of pro-creating individuals" the population will approach more closely to the homozygous condition, *i.e.* its total *potential variability* will have been lowered. Theoretically the potential variability of a freely intra-crossing population should remain undiminished, but under natural conditions a reduction is made possible by the action of selective agents. Selection, therefore, constitutes the primary cause in determining the ultimate adaptive characters for which an ecotype will become stable; moreover it induces stability by intensifying the isolation of certain genotypes, thus hastening an automatic reduction of potential variability. The chance elimination of genes responsible for the expression of tolerant characters would also tend to an automatic increase in their homozygosity. The comparative uniformity, so striking a feature of many allogamous ecotypes, can, therefore, be attributed primarily to the restrictions placed by the factors of the environment on inter- and intra-ecotype crossing.

On the other hand, in strictly autogamous populations a theoretical decrease of 50 per cent. in potential variability would occur automatically in each successive generation following a chance cross. It should, therefore, be possible to find a habitat occupied by a population, which as a whole possesses potential variability but is composed of numerous distinct homozygous groups each lacking potential variability. But even

a population so constituted would be liable, when natural conditions set a limit to the number of individuals occupying a given space, to a reduction in potential variability, owing to the possible disproportionate elimination, by environmental influence and by chance, of certain genotypes, resulting ultimately in the extinction of some of the pure lines.

Influence of climatic, edaphic and biotic environmental factors.

It is well known that climatic environment determines to a considerable extent the type of vegetation in any particular region, and that, in general characteristics, the floras of geographically distant but climatically similar areas bear a resemblance to each other, although their component species may be quite distinct. Recent investigations have shown that the components of a single species-population are not distributed indiscriminately over different climatic regions, but group themselves into ecotype zones which bear a relationship to their climatic environment. This phenomenon is particularly well illustrated in cases where there is a repetition of climatic ecotype zones in widely separated areas, *e.g.* the zonation of *Armeria vulgaris* on the coasts of Norway and Greenland (Turesson, 1922).

Under natural conditions the distribution of climatic ecotypes may be either in a latitudinal, meridional (see Turesson, 1931, p. 148), or, as can be observed when passing from the lowlands to alpine situations, in a vertical direction. The different ways in which ecotype zones may be formed are, according to Sinskaja (1931, p. 58), as follows:

"(1) Continuity in zonal variability [of characters] is naturally formed in the course of the migration of the complex of types from one common focus in the direction of a gradual change of climate.

(2) Zonal localisation may arise as a result of the contact of two climatypes [climatic ecotypes] (or species) spreading from two different foci, so as to meet each other. In this latter case an intermediary zone of types may occur due to the recombination of characters. However, no such gradualness or continuity in the variability of the geographical characters can be observed here as in the first instance, and besides differences between extreme zones are also revealed in non-geographical characters."

As an example of the first type of zonation Sinskaja cites the conclusions from her work on Eurasian forms of *Camelina*, whose migration took place, according to the available data, from one centre and proceeded in a south-east to north-west direction; and as an example of the second type of zonation she instances the discovery in East Asia of transitional stages between European and Japanese radishes.

Peculiar habitat conditions within a climatic zone may, however, be conducive to the development of intra-zonal ecotypes, *e.g.* the edaphic differentiation of *Hieracium umbellatum* L. into one type on the shifting dunes and another distinct type, which differs from it in the extreme prostrateness of its stems, on the adjacent arenacious fields (Turesson, 1922, p. 334).

That peculiar edaphic conditions are sometimes responsible for the existence of ecotypes beyond their normal distributional range is suggested by the appearance of more southern forms on chalk, as instanced by Sinskaja (1931), and by the statement of McConnell (1919, p. 125) that the "Old Red Sandstone soils generally are said to ripen wheat furthest north of any in Scotland."

Both climatic and edaphic conditions can, however, on occasion be materially altered by the activity of plant and animal agencies, in consequence of which peculiar local environmental conditions are realised, *e.g.* those obtaining in woodland associations where specialised shade ecotypes, such as *Dactylis glomerata* var. *lobata* Drej., occur. The maintenance of pasture conditions in Britain is largely the result of biotic agents, since much of the pasture land would, if freed from the influence of herbivorous animals and rodents, revert to woodland, with the consequent creation of a new biotic sub-environment.

The examples briefly recorded above are sufficient to indicate the important part played by the individual environmental factors in the distribution of ecotypes. It is nevertheless the combined, though not necessarily equally intense, action of all the environmental influences which contributes to the success of the genotypes in a habitat.

II. The ecotype concept in relation to agriculture: a classificatory scheme for crop plants.

It seems reasonable to suppose that, since the environmental conditions are in great measure responsible for the distribution and grouping of biotypes under natural conditions, the same control will be exerted upon the distribution of crop plants. But it must be borne in mind that, whereas the process operates in the wild by the continual interactions and adjustments of the plants concerned to the habitat conditions, in agriculture man can so influence the environment by cultural treatment and the elimination of competition, that he can frequently adapt the habitat to permit of the success of a particular crop. The two processes are essentially similar in that the end result is the attainment of equilibrium between the habitat conditions and the inhabiting forms. But even in agriculture there are limits to the possible extension of the range

of particular plants beyond the ecological regions prescribed by nature; yet before these limits are reached it may not always be economically advisable to endeavour to transform the environment to suit the plant, but rather to utilise plants inherently fitted for the existing environment.

The mapping and description of natural vegetation, and the study of plant associations, while they are of great general importance to the agriculturist, have so far had little direct influence on agricultural practice. The study of subspecific units in relation to environment, however, by emphasising the error of assuming a single ecological formula for each species, brings the application of ecological methods into immediate touch with the requirements of agriculture.

The agrotype.

The obvious parallelism between the processes underlying the ecological grouping of plants in the wild and the regional preferences exhibited by crop varieties suggests that some of the latter are in reality ecotypes, though many others represent smaller units distinguished by characters of an economic rather than an ecological significance. These smaller units are often more nearly equivalent to the geo-ecotype than the ecotype as defined by Turesson (1922), with the difference that, whereas the geo-ecotype arises from chance isolation of a part of a larger population, possibly an established ecotype, the agricultural variety more usually represents the result of conscious fractionation of a genotype complex accompanied by controlled isolation of the parts. This artificial selective influence which, even when applied to a natural ecotype, tends to a more or less rapid reduction in potential variability and to a consequent proportional change of type, which may or may not be parallel with previous environmental selection, affords a reason for distinguishing between the cultivated *agrotypes* and the natural ecotypes. An agrotype, moreover, is, under certain agricultural practices, more liable to extreme environmental fluctuations than are the units in the wild. In the case of a genotypically diversified agrotype of, for example, a pasture crop, the pasture is its natural (and economic) habitat; but, under pasture conditions, reproduction by seed is limited to such an extent by the grazing animal that an artificial habitat must be created for the purpose of reproduction. The environmental conditions prevailing in the latter habitat are materially different from those of the former, and may in time so influence the numerical frequency of the genotypes that successive generations will become less valuable for pasture purposes, cf. relevant paper by Levy and Saxby (1932). This distinction between the natural

and the seed habitat is further accentuated when an agrotype, intended for a particular environment, is seeded in a climatically distinct region, *e.g.* the mangel crop (*Beta maritima* L.).

The assumption that, while natural selection tends to favour the type best able to propagate itself under a given environment, artificial selection strives to satisfy economic needs (cf. Kemp, 1929) has therefore an important bearing on the procedure to be employed in the preservation of a genetic constancy in crop units. This is particularly so in those heterogeneous units where (1) vegetative production rather than seed reproduction is concerned, (2) two distinct environments are necessitated by agricultural practice, or (3) where the unit is a perennial and therefore subject to seasonal environmental fluctuations. Under these circumstances an agrotype might, in course of time, become so altered as to be unrecognisable, consequently some control of stock-seed production is advisable in order to maintain the constituent genotypes at the required equilibrium. Intra-fertilising agrotypes, therefore, cannot be regarded as static under every environment, but rather as dynamic units liable to genetic change in response to alterations in the intensity of selection conditioned by the environmental factors of their habitats.

It might be argued that, since the influence of man is undoubtedly an environmental factor, his needs constitute part of the ecological conditions imposed upon a crop variety. But, since the requirements of man may lie in a direction opposed to the natural processes of environmental control, any system of crop plant classification must perforce give preference to the characters of economic importance. Allowance must also be made for the fact that popular fancy lends an economic value to many characters of no ecological worth. Units possessing differences of such a nature cannot be regarded as separate ecological units though they obviously must receive agricultural recognition, and so for these the term agrotype has already been suggested on page 213 of the present paper.

The agro-ecotype.

The ecological preferences of crop plants, however, must not be underestimated, since, even if optimal cultural conditions were to cause the economic differences between agrotypes to assume a greater agricultural significance than the differences of strictly ecological value, the reverse might be the case under more extreme conditions. In the majority of cases agrotypes could be grouped into larger units—*agro-ecotypes*—according to their ecological preferences.

The description of agrotypes.

Undoubtedly the classification of obligatory cross-fertilising crop plants presents one of the most difficult problems, because such groups might be expected to contain several genotypes exhibiting a number of different character combinations which could not, individually, be utilised for purposes of identification. Nevertheless, provided that during the seed-raising processes these intra-breeding populations are maintained under strict isolation, they may form valid agricultural units embodying the environmental preferences of their component parts. Under the prevailing strictly observational system of morphological differentiation it is extremely difficult, in many cases impossible, to provide a distinctive description, *e.g.* for some of the forage crop varieties. However, varieties which are considered to be morphologically indistinguishable from each other by customary methods of examination may possess dissimilarities of agricultural importance. These circumstances have led Kirk (1931) to advance the proposal that new varieties should be accepted for registration on the basis of economic superiority only and that the lack of a *distinctive* morphological description, or the occurrence of morphological heterogeneity, should not necessarily preclude them from registration. Such a criterion, if it were correlated with the administration of a stock-seed or habitat certification, would afford a means of dealing with agrotypes, including established local races of known ecological adaptation, which present peculiar difficulties as to their identification. This scheme, therefore, would constitute a useful step in a comprehensive system of registration.

Nevertheless, it should be pointed out that there is an urgent need for more exact methods than those commonly employed in the evaluation of morphological and physiological characters, *e.g.* length and breadth of leaf, etc., time of flowering, water requirements, etc. The utilisation of statistical methods in comparing varietal descriptions suggests a possible alternative to the profuse employment of adjectives which so frequently leads to descriptive ambiguity. Not only would statistical treatment involve the exact measurement of characters which could then be expressed in mean values and thus afford a way of comparing one heterogeneous population with another, but it would also supply data for the calculation of variability within each population. Statistical data could only be obtained from cultures of the individual components of a population, a condition which would necessitate the cultivation of a number of spaced plants representative of the population as a whole.

The grouping of agrotypes into agro-ecotypes.

In this proposed classification of crop plants the intra-fertile agrotypes, which represent the ultimate units of the system, would be grouped into ecological units or agro-ecotypes. The division of the latter units into climatic edaphic and biotic agro-ecotypes is, however, neither practicable nor desirable. These three main classes of environmental factors can, nevertheless, be utilised to indicate the combination of environmental preferences exhibited by the individual agro-ecotype, as is very briefly illustrated in the following hypothetical example.

Herbage plants.

Agro-ecotypes	Environmental preferences			Described agrotypes
	Climatic	Edaphic	Biotic	
A	Northern, dry	Limestone	Pasture	*a, b, c, d*
B	Northern, dry	Limestone	Hay	*e, f, g*
C	Northern, moist	Peat	Pasture	*h, i*
D	Northern, moist	Peat	Hay	*j, k, l*

The administration of the scheme.

The following scheme for the administration of the proposed classification is suggested.

First, the organisation of a *State Institute* possessing facilities such as those at present obtaining at the National Institute of Agricultural Botany in England, and at the Plant Registration Station in Scotland. The duties of such an institute would be (1) the compilation and publication of *standard* descriptions of agrotypes, based on data obtained at the institute and incorporating information collected from regional trials regarding environmental preferences; (2) the grouping of agrotypes into agro-ecotypes; (3) the interchange with other state institutes of descriptions and data concerning these units; (4) the testing of units established by other state institutes, if their recorded ecological preferences suggest that an examination is advisable; and (5) the certification of stock-seed crops of registered agrotypes.

By centralising the compilation of descriptions and not entrusting it to individual workers situated in different ecological regions, the danger of describing different reaction types of the same genotype would be obviated. Promising new crop types would be submitted for examination, as at present, to the state institute by breeders within its sphere of influence, the institute being responsible for the naming and the publication of standard descriptions of the agrotypes which proved to be worthy of recognition.

Second, the co-operation of *District Institutes*, such as the existing agricultural colleges or other recognised institutes situated in different ecological regions. The purpose of these would be to observe the behaviour, under local conditions, of material supplied to them by the state institute: these data would be appended to the standard descriptions compiled by the state institute. The work of the state and district institutes should, whenever possible, be accompanied by adequate meteorological observations.

A complete survey of the agricultural crop units at present in cultivation, an investigation which under prosperous financial conditions might be desirable, is not, in the circumstances, a practical proposition. However, a definite advance in the methods of crop plant registration along the lines suggested seems possible, if attention were to be confined to varieties for future introduction, employing for comparison a limited number of the best varieties of the respective crop plants now in existence. Such a scheme, if adopted even within the limits of the British Empire, would make available to research workers and agricultural advisory officers reliable information regarding the crop plants produced in this area. If, however, a standard system of genecological nomenclature for agricultural crop varieties were to be accepted internationally, the exchange of material would be greatly facilitated. An international scheme would require the services of an *International Institute* as, for example, the existing organisation at Rome, acting as a central station for the recording and periodic publication of the data submitted to it by the state institutes situated in the various countries.

In a suggestive article on international agro-ecological research, Bensin (1930) proposes an international terminology for local variety types, but it is questionable whether his (Bensin, 1928) voluminous terminology will achieve the desired result. Such a proposal, however, has much to recommend it as an aid to the grouping of agrotypes into agro-ecotypes and as a means of facilitating the brief general summarisation of the detailed statistical descriptions of agrotypes submitted to the international institute by the state institutes.

Genecological crop units of greater magnitude.

It must be realised that within a single crop other genecological units occur where individual identities are maintained chiefly on account of their sterility relationships, or by the insufficient viability of hybrids.

Since morphological similarity is not an infallible guide to inter-fertility, *e.g.* the two intersterile groups, with 14 and 42 chromosomes respectively, within *Phleum pratense* L. (Gregor, 1931), the differentiation of these units cannot be adequately accomplished by the utilisation of morphological and ecological criteria alone, and therefore cytological and experimental investigation is necessary. The actual delimitation of these larger groups into *ecospecies* and *coenospecies* must, however, remain the function of the research worker, as they are beyond the prescribed scope of the state institutes.

III. Summary.

(1) The ecotype concept as formulated by Turesson (1922) postulates the existence, in the wild, of sub-specific units—ecotypes—which result from the environmental fractionation of a larger population. Details are given of the occurrence of these units in nature.

(2) While the wild ecotypes are not strictly comparable with the agricultural crop units yet the general principles underlying this concept have a definite agricultural application. Suggestions are made for a standard system of crop classification which embodies data relating to the environmental preferences of its units. Two units of agricultural significance are discussed: (1) the *agrotype*, or ultimate crop unit, and (2) the *agro-ecotype*, or group of agrotypes possessing similar environmental preferences. The measures necessary for the administration of the scheme are briefly outlined.

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Reflections Concerning New Crop Varieties.

IMPERIAL BUREAU OF PASTURES AND FORAGE CROPS,
ABERYSTWYTH, GREAT BRITAIN.

REFLECTIONS CONCERNING NEW CROP VARIETIES

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INTRODUCTION

Within recent years much has been written concerning the general ecology of grasslands and the adaptation of grassland constituents. Although the observed effects of ecological factors operating over long periods of time, as in the case of natural and semi-natural pastures, indicate the trends of natural adaptation to environment they do not provide an infallible guide to the agricultural conditions under which these adaptations will attain their greatest usefulness. Only rarely are the inherent ecological attributes of crop varieties directly studied in relation to a variety's maximum utility under the more or less artificially controlled environment of cultivation. In the present article it is therefore proposed firstly to compare the ecological units of the wild with their agricultural equivalents, and secondly to suggest possible means of increasing grassland production by making the fullest economic use of the available ecological peculiarities of new varieties.

THE ECOTYPE CONCEPT AND ITS AGRICULTURAL SIGNIFICANCE

The term *ecotype* was proposed by Turesson in 1922, and as an abstract concept it has since then invaded plant breeding literature. Particular ecotypes are seldom mentioned, the term generally being used to denote a population which, it is assumed, is specially adapted to its habitat. It is, however, curious that while the implications of the ecotype concept have been readily appreciated and have already considerably influenced plant breeding technique, the nature of the unit itself and its relationships to other units have received so little attention.

In the sense of Turesson an ecotype is a population which has become differentiated in response to the environmental conditions of its habitat. The occurrence of races of similar appearance in separate localities of similar environment is suggestive of the ecotypic fractionation of a larger population. However, it would be a misrepresentation of natural phenomena to regard all kinds of local differentiation as indicative of habitat differentiation. The conjunction of habitat and habitat type may have reference to some characters and not to other, perhaps more striking ones. The same ecotype therefore is not necessarily genetically uniform over its entire range. Even in respect of the ecotypic characters themselves populations are seldom clearly delimited, and diagnosis of an ecotype is largely dependent on the determination of the proportional representation of "indicator" characters. For example, in the Sea Plantains of Britain the distribution of growth-habit types results from the action of environmental factors such as grazing, exposure to high winds, etc. Growth-habit is therefore regarded as an ecotypic indicator character of diagnostic value.

Thus the ecotype *decumbens* is represented by populations where decumbent growth-forms predominate, and similarly *ascendens* by populations where ascending individuals are in the majority. It should be emphasized, however, that growth-habits form a continuous series ranging from the extreme decumbent to the extreme erect, and according to the prevailing habitat conditions different points on this series attain predominating frequencies, and impart individuality to populations without sharply delimiting them as ecotypes. Provided a sufficiency of varied habitats were available, the average growth-habit of populations would present a continuous ecological trend or *ecocline* to use Huxley's terminology. These considerations make it imperative to study both the spatial and ecological relationships of characters before concluding that a population represents an ecotype in the sense of Turesson.

Numerous examples of the occurrence of racial differentiation in contiguous valleys and even in one and the same valley, unaccompanied by discernible ecological differences are cited by Crampton in his monograph of the snails inhabiting Tahiti. It is extremely improbable that all these differentiated populations are specialized to different habitats. What is more likely is that chance differences in the frequencies of genes at the time the various populations were founded have influenced the ultimate population characters. Such predetermined differentiation is not ecotypic in the strict sense of the term as it apparently arises from the chance fractionation of a parent population. Because populations of this kind are often comparatively uniform genetically, and because their predominant characters are at least tolerant of the prevailing environment, they are valuable to the breeder.

It is also inadmissible to assume without experimental evidence that if a population is found to possess characters of demonstrable ecotypic significance, these characters are optimal for similar habitats elsewhere. For example, in coastal regions where Sea Plantains are more or less continuously distributed, size and growth-habit have been found to be controlled by environment. Inland, however, some relatively dwarf populations exist in isolated lowland habitats which, by analogy with similar habitats near the coast, might be expected to support large sized plants. But there is evidence to show that these inland habitats have been populated with local migrants from mountain localities where large size is absent. It would therefore almost certainly be incorrect to conclude that in such cases dwarf habit has been favoured at the *expense* of tall habit. After due regard is given to the probable genotypic limitations of the original migrants it would be equally inappropriate to use local distributional anomalies of this kind to discredit the ecological significance of the character concerned.

There are, moreover, widespread characters which affect all ecotypes occurring within their sphere of influence. For example, an anthocyanin leaf spot gives regional character to the Sea Plantain ecotypes occupying northern Europe and eastern North America.

It may not be far from the truth to say that amongst non-vegetatively reproducing plants a type's optimal environment is that in which seed reproduction reaches

its maximum expression. Nevertheless in most habitats preferential, as opposed to maximal, seed production must play a major role in establishing the predominant characteristics of populations. These characteristics, even when their ecotypic significance is unquestionable, might have little direct economic value. For instance, it is conceivable that a decumbent ecotype of *Lolium perenne* developed in response to prolonged grazing might be economically inferior, even in its own locality, to a more erect variety of greater vegetative vigour. Similarly, in a variety grown for its seed the environment of maximum reproduction is not invariably its optimal *economic* environment, e.g. the value of a barley variety is judged by its productivity and quality, not by yield alone. Since ecotypic specialization and economic utility do not always run parallel to each other the value of ecotypes to the plant breeder is more likely to lie in their usefulness as a source of material for the production of bred strains than as a direct supply of commercial seed. The established regional races, e.g. of *Phleum pratense* in Scotland and *Trifolium repens* in England, are the nearest agricultural equivalents of ecotypes. But differential cultural treatments and periodic reseeding within a region tend to interrupt or prevent the formation of a regional ecotype. The bred strain corresponds still less to the natural ecotype, representing as it does a comparatively uniform population which has been consciously selected to a preconceived standard and whose environmental preferences have to be later determined by trial. Undoubtedly ecological preferences determine the general distribution of crop plants, but they are not the ultimate determinants of a variety's usefulness. For instance, if the economic characters of a variety do not attain a prescribed standard in a habitat it is not, commercially speaking, fitted to this environment. Thus ecological attributes become subordinated to economic demands, and the gap between the ecotype and its agricultural equivalent is still further widened. It would therefore be unfortunate if the term ecotype were to be applied indiscriminately to categories of such different meaning and origin.

Notwithstanding the inconsistencies of the basis of assessing a population's fitness to its habitat, the concept of ecological control of plant distribution obviously retains its agricultural significance. But if the term ecotype were to be interpreted in its agricultural sense it would be deprived of much of its significance as a unit in a genecological classification of wild populations. In consequence, and to avoid the inappropriate use of the term ecotype in agricultural literature, the prefix *agro-* might with advantage be added to the ecological units of cultivation. This *agroecotype* would be described not in terms of its morphology but with reference to the cultural environment under which it may be expected to attain its usefulness, i.e. in terms of the general climatic, edaphic and biotic conditions and farming practice of such an agricultural environment. As far as herbage plants are concerned their cultural environments might be very broadly indicated by descriptive headings like upland-pasture, upland-pasture-hay, lowland-pasture, etc. A nomenclature of this kind could be applied conveniently to the main agroecotypic categories. Thus the description of a particular upland-pasture agroecotype might read as follows :

UPLAND-PASTURE, I.

Climate, northern insular, summer and winter temperature differences slight, rainfall 28 to 36 inches ;

Soils, poor mineral, winter water-table high ;

Biotic environment, bottom grass in closely grazed pastures ;

Farming practice, 4 to 6 years pasture, aerial competition detrimental, sow under grazing nurse crop, flowering July.

Different species possessing races which are useful under similar conditions would therefore have analogous agroecotypes. This is particularly likely to occur in herbage plants where varieties of unrelated species can be chosen to fulfil the same purpose. For instance, upland-pasture agroecotypes of *Cynosurus cristatus* and diploid *Phleum pratense* might be found to have practically identical descriptions. It is important to note, also, that an agroecotype may comprise more than one agricultural variety of the same species, where the varietal distinctions are based on economic or even arbitrary characters quite without ecological significance, e.g. Red and White Fyfe wheat. The variety and not the agroecotype is therefore the ultimate crop unit. Since some populations, especially populations of cross-fertilizing plants, are often indiscriminately referred to as strains or varieties it would seem advisable to adopt a single term such as *agrotype* for all agricultural populations which are placed on the market, whatever their degree of morphological distinctness. An account of the conditions under which these agrotypes reach their greatest agricultural utility, together with brief descriptions indicating their diagnostic and economic characteristics would be essential not only for assessing agroecotypic relationships but as a means of recording available crop plant material. The ever-increasing specialization of crop plants resulting from the efforts of plant breeders suggests that in the near future some such scheme of crop classification will be required for the guidance of farmers, merchants and plant breeders themselves.

THE ECONOMIC UTILIZATION OF NEW HERBAGE VARIETIES

It may well be that in order to increase grassland production by the use of specialized varieties, specialized seeds mixtures and systems of grazing will have to be adopted. At the present time it is usual to regard new herbage varieties merely as components of multiple grass-species seeds mixtures. But there is no reason for assuming that they will attain their greatest usefulness either in the orthodox seeds mixture or in the customary all-the-year-round pasture. In theory a suitable plan of management for pastures composed of complicated seeds mixtures can easily be visualized. But in practice seasonal peculiarities and the needs of stock not infrequently make the strict adherence to a preconceived ideal a practical impossibility. In a dry spring, for instance, when grass is scarce, excessive grazing of pastures is unavoidable although it may be fully realized at the time that the treatment is detrimental to the grasses expected to produce fodder later in the season. A complicated seeds mixture thus obviously contributes to the difficulty of maintaining an effective system of pasture control.

The remedy then would seem to lie in the simplification of mixtures and the provision of pastures where only species and varieties of similar growth rhythm would be associated. In this respect we might imagine a sequence of specialized mixtures where all species in any one field develop simultaneously. Under such a system the over-grazing of early species would in no way interfere with the species relied on for later use. But even here interspecific competition and the possible effects of selective grazing would still be operative. Therefore, to reduce even more the variables which it is the object of management to control, the mixture might be further simplified and comprise only varieties of a single grass species. For example, a top- and bottom-grass variety of early cocksfoot for spring grazing, a ryegrass mixture for later, and a timothy mixture for midseason grazing. These in turn would be followed by the grazing of their aftermaths in successive order, or as occasion demanded. Such treatment should minimize the risk of a fodder shortage at critical times and might actually supply a greater annual bulk of herbage than an equal area of pasture arranged on orthodox lines.

Similarly, the advent of specialized varieties may in time influence the general methods of land reclamation. It may be as well to mention that there are here two distinct problems : the reclamation of open hill grazings, especially those at elevations above the limit of profitable arable cultivation, and the reconditioning of enclosed lands now in poor pasture. Until it is appreciated that many of the latter are, in their present deteriorated state, useless as arable land, or even for productive pasture, the importance of reconditioning will remain over-shadowed by hill-land reclamation, which appeals more to the popular imagination. Numerous methods of land improvement have been recommended, but the usefulness of any particular method depends largely on local circumstances. The use of the plough, however, is becoming increasingly advocated. Although on many upland farms, ploughing of the enclosed grassland still presents relatively few difficulties, considerations of finance, labour supply or climate make even temporary additions to the arable acreage impracticable. Therefore, under these circumstances, renovation, to be economically successful, must avoid the customary interim period of rotational cropping.

A serious deficiency of the minerals essential for the growth of the valuable pasture plants is a common feature of degenerate pasture lands. Obviously the first consideration in a programme of renovation is to apply sufficient manure to ensure the establishment of the plants sown. But to attempt to raise the fertility of the top nine inches of soil to this level at one application frequently necessitates heavy initial expenditure. It would therefore seem to be advisable to spread the cost over a period of years by concentrating on the fertilization of the top few inches only. The subsequent ploughing down of an improved herbage would automatically fertilize the lower layers.

Renovation by stages of progressively more productive pastures, each stage growing under a minimum application of artificial manures, has economic possibilities provided some financial return is obtainable during the process. For the experiments being conducted by the Scottish Plant Breeding Station at their upland Sub-Station* three stages have been planned as follows :—

*Ainville Sub-Station is situated 12 miles S.W. of Edinburgh at an elevation of 900 feet.

Stage I, a pasture consisting of large-seeded annuals e.g. varieties of oats and wheat, capable of growth under the poor conditions of soil tilth so often encountered after old pasture has been ploughed.

Stage II, a predominantly *Trifolium repens* pasture, or soil-fertility raising phase. Special attention has been paid to grass varieties with a growth rhythm coincident with that of wild white clover in view of the fact that clover makes but slow growth in the spring at high altitudes and under conditions of low soil fertility.

Stage III, a long duration pasture comprising perennial species of high productivity. The use of grazing annuals as nurse crops in stages II and III has provided satisfactory grazing without injuring the establishment of the more delicate perennial species.

Ultimately it should be possible to link up these practical considerations with the somewhat more theoretical aspects of the problem previously discussed, by recording the ecological attributes of new varieties in terms of their usefulness in cultivation. There is no doubt that the introduction into commerce of specialized varieties has increased the opportunities for agronomic research. And until this research can make available to the farmer information concerning the cultural conditions under which new varieties may be expected to attain economic value, he, as Watson points out, "will be left to discover for himself, often by a costly series of trials and errors, the particular new varieties that constitute, for him, improvements on the old."